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II. Variation and Correlation of the Number of Umbel Rays of some Umbelliferæ. By C. Cool and A. N. Koopmans. (With Plate I and Three Diagrams in the text)

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JOURNAL OF ANATOMY AND PHYSIOLOGY

THE STRUCTURE OF THE BLASTODERM, AND THE CONTINUITY OF THE CELL-ELEMENTS DURING THE EARLY STAGES OF DEVELOPMENT.

By J. CAMERON, M.D., D.Sc., *Professor of Anatomy, Dalhousie University, Halifax, Nova Scotia*; and R. J. GLADSTONE, M.D., F.R.C.S., *Senior Demonstrator and Lecturer on Anatomy, King's College, University of London.*

1. INTRODUCTORY.

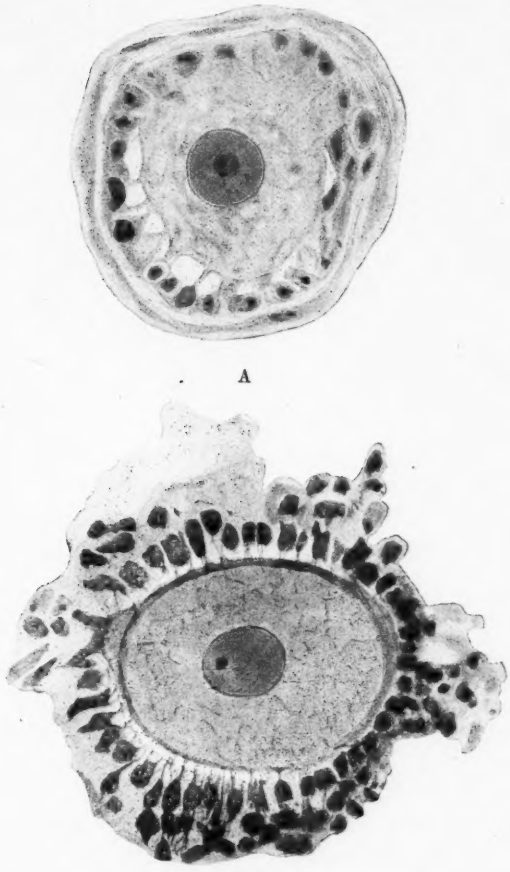
THE conception of a general continuity of the protoplasmic elements which form the tissues of all living organisms is by no means new. It preceded the "cell theory," and although "cells" have for many years been regarded as "independent units, each having its separate life-history," there has always existed a considerable number of observers who, while not questioning the theory of separate cells, have described *organic continuity* of the cell-elements in the particular organ or tissue which they have specially studied. Thus Sedgwick (28) in Peripatus and in chick embryos, Graham Kerr (17) in tracing the continuity of developing nerves with muscle in Lepidosiren, Bernard in his researches on the structure of the retina, Studincka (30) and F. E. Schultze (26) in studying the structure of epithelial cells, have all been led to the same conclusion, namely, that there is a general continuity of the cell-elements in these tissues. Some of these writers, notably Sedgwick and Bernard, have extended the conception of continuity of the cell-elements in the tissues which they specially examined to continuity of the cell-elements in general.

Wilson (33) has pointed out and emphasised the very important fact that in Amphioxus and Echinoderms "the results of experiments on the early stages of cleavage are difficult to explain save under the assumption that there must be a structural continuity from cell to cell." This conclusion is supported by the work of Hammar (10) on the ova of Echinus.

More recently, Hardesty (11) in the nervous system, Godlewski (9) and M'Gill (20) in muscle tissue, His (14) in epithelia, and Spalteholz (29) in the connective tissues, have demonstrated the continuity of the cell-elements in these different forms of tissues. Notwithstanding the evidence brought forward by these and by many other observers, the theory that all living tissues are built up of *independent* units called "cells" is still almost universally held, and that the "cell" is in Brücke's words "an elementary organism" (3).

In tracing the history of the cell-theory which was promulgated by Schleiden (25) and Schwann (27) in 1838 and 1839, we find that Heitzmann (13), so long ago as 1873, contended that cell-division is incomplete in nearly all forms of tissue, and that even when cell walls are formed, they are traversed by strands of protoplasm, by means of which the cell bodies remain in organic continuity. The whole body was thus conceived by him as a *syncytium*, the cells being no more than nodal points in a general reticulum, the tissues thus forming a continuous protoplasmic mass.

It has been conclusively demonstrated that in nearly all plant tissues the cell walls are traversed by delicate intercellular protoplasmic bridges, whilst in the case of animal tissues many observers have described the existence of similar bridges, one of the most familiar examples being the so-called "prickle cells" of the stratum Malpighi of the skin. These will be described later in detail when we come to deal with the structural features of epithelial tissues. A more important example is furnished by the protoplasmic connexions of the cell-elements of the corona radiata, not only with each other but actually with the ovum itself. This structural continuity, which has been already demonstrated by Flemming (8), Heape (12), and Retzius (23), is illustrated in fig. 1, which shows two stages in the evolution of the ovarian ovum of the cat. In the early stages (A) it will be noticed that the oöplasm is directly continuous with the cytoplasm of the surrounding cell-elements. This appearance is made more manifest by the fact that the ovum possesses no zona pellucida at this stage, though the continuity is still distinct even in the later stages (B). This observation is of the utmost importance in relation to the question of the inheritance of acquired characters, for it is not in agreement with the theory of the immutability of the germ plasm, postulated by Weismann (32), and upon which his theory with regard to the non-transmissibility of acquired characters has been largely founded. It seems to us that the organic continuity we have described between the germ plasm and the cytoplasm of the "somatic cells" must surely mean that the former is liable to be influenced by the latter, apart from the nutritive function, which is generally admitted. We hope to prove in a subsequent paper that the



A

B

FIG. 1.—Two stages illustrating the development of the ovarian ovum and Graafian follicle in the cat. A shows an early stage, before the complete development of the zona pellucida. It will be observed that the cytoplasm of the follicle cells is continuous, not only with that of the ovum, but also with that of the adjacent cells of the same layer, and of the ovarian stroma. B, later stage, in which it will be noted that the zona pellucida now forms a distinct boundary zone, but does not completely separate the ovum from the cells of the corona radiata. Processes from these cells pass through the zona pellucida, and are continuous with the cyto-reticulum of the oöplasm.

"germ cells" have a similar relation to the surrounding "somatic cells" in the male also.

It will be our aim in this memoir (to which the present paper is merely an introduction) to demonstrate that—

(1) It is the nuclei with their contained chromatic material which should be regarded as units, rather than the cell-elements.

(2) There is an organic continuity between the cell-elements of the connective tissues, the cell-elements of the central and peripheral nervous systems, and in certain epithelial layers.

(3) This continuity is in most cases primary, and not secondary.

(4) The so-called intercellular substance[1] forms an essential part of this continuous *living* tissue, which with its contained nuclei forms a *plasmodium*.

The connexion of cell-elements together by means of delicate filaments continuous with the cyto-reticulum and nuclear network of the individual cells was demonstrated in the retina by the late Mr H. M. Bernard (2). This author afterwards extended his observations to other tissues, and described a continuous network of linin threads, uniting and passing through the cell-elements. This he termed a protomitomic system. Further, he considered nuclei to be aggregations of chromatin at the intersections of the linin network.

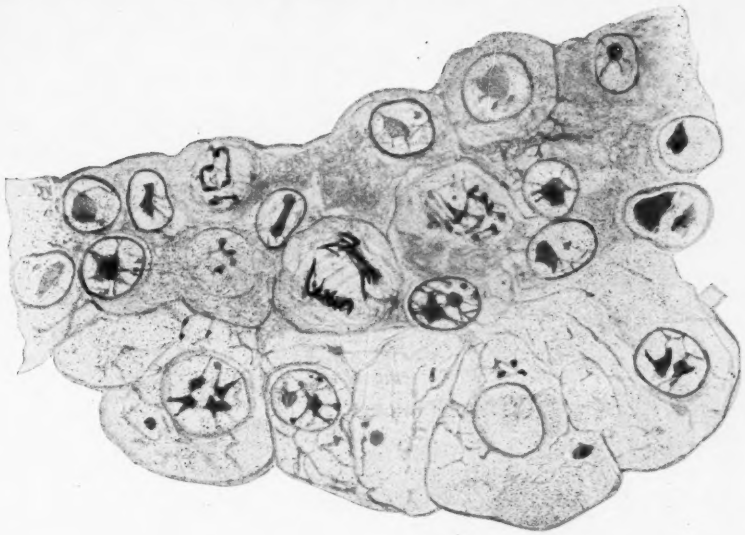
Our views in the main accord with those of Bernard. Our observations, however, indicate that the mode of continuity between neighbouring cell-elements is not necessarily through the linin network alone, but also by a direct continuity of the cytoplasm, *which has existed from the very first.*

2. The Early Ovum.

It is well recognised that in the early stages of segmentation of amphibian and avian ova the division is incomplete. For example, the divisional planes in the segmenting cicatricula of the bird's ovum do not involve anything like the whole thickness of the cicatricula; and what is more significant still, it may be noted that these planes do not extend peripherally into the periblast, as is well shown in the excellent micro-photographs by Miss Blount in Lillie's book on the development of the chick (18). Fig. 2 is a drawing of a small portion of the ectoderm near the yolk wall, from a transverse section through a chick embryo, incubated eighteen hours. The section passes through the primitive plate, a short distance behind the primitive groove, and shows, above, the ectoderm.

[1] We do not regard as living material, calcareous matter deposited in the matrix of bone, or other inert substances deposited in the ectoplasm.

This consists of fairly well defined cell-elements, which are mapped off by thin partitions of darkly stained protoplasm, directly continuous with the cyto-reticulum of the adjoining cell-elements, and also with the protoplasm filling in the angular spaces between these. There are no



W. CHAMPNEYS.

FIG. 2 is a drawing of a small portion of the ectoderm and entoderm, near the yolk wall, from a transverse section through an eighteenth-hour chick embryo. The section passes through the primitive plate, a short distance behind the primitive groove. The ectoderm is shown above. This consists of well-defined cell-elements separated by thin partitions of darkly stained protoplasm, which is directly continuous with the cyto-reticulum of adjoining "cells," and also with the protoplasm filling in the angular spaces between the cell-elements. There are no clefts in these partitions, nor can the partitions be regarded as cement substance; for, as is clearly shown in the large underlying entodermal cell-elements, they are continuous with and have the same structure as the strands of the cyto-reticulum or spongioplasm. The faintly stained entodermal cell-elements have a remarkable appearance in contrast with the more deeply stained ectodermal layer. They appear to be distended with a clear achromatic cytoplasm, almost identical in its physical characters with the nucleoplasm. After a careful study of this material we are convinced that it is a protoplasm extruded from the nuclei in a *nascent* condition, in virtue of which it is achromatic in its reaction to staining agents. Drawn under an $\frac{1}{2}$ apochromatic objective with compensating ocular × 7.

clefts in these partitions separating adjacent "cells," nor can the partitions be regarded as cement substance, for, as is clearly shown in the large underlying entodermal cell-elements, they are continuous with and have the same structure as the strands of the cyto-reticulum or spongioplasm.

The faintly stained entodermal cell-elements in fig. 2 have a remarkable appearance, which contrasts with the more deeply stained ectodermal layer. They appear to be distended with a clear achromatic cytoplasm, almost identical in appearance with the nucleoplasm. After a careful study of this material, we are convinced that it is a protoplasm extruded from the nuclei in a *nascent* condition, in virtue of which it is achromatic in its reaction to staining reagents. This nascent non-staining cytoplasm can be demonstrated also in the entypy stage of the mouse embryo (fig. 10), where it exhibits itself in the form of clear achromatic zones immediately surrounding the nuclei or as clear refractile globules in the general protoplasm. This appearance is likewise characteristically shown in the

FIG. 3.—Segmenting ovum of *Echinus esculentus*, sixteen-cell stage, showing blastomeres surrounded by a continuous "ectoplasmic layer," which forms a connecting medium between the cells, and, in conjunction with these, constitutes a "complete organism," or "individual," as distinguished from a "cell-colony," united by an extraneous "cement substance."

deeper layers of the trophoblast of the chorionic villi (fig. 14). One of us has previously demonstrated the extrusion of this nascent achromatic cytoplasm from the nuclei of the developing retina (4 and 5) and brain (6).

The continuity of the cell-elements of the morula mass may also be observed in invertebrate ova. For example, fig. 3 is a drawing which one of us executed whilst studying the fertilisation and segmentation of the ova of *Echinus esculentus* at the Millport Marine Biological Laboratory in 1903. In the morula stage of development of this species it can be clearly recognised that the blastomeres are held together by a thin layer of homogeneous protoplasm which exhibits itself as a very delicate achromatic zone surrounding the periphery of the morula mass. Hammar (10) has, moreover, shown that in another species of Echinus (*E. miliaris*)

the segmenting ova possess what he terms an ectoplasmic layer which not only surrounds the blastomeres, but can also be traced deeply between these elements. He was able to demonstrate this "ectoplasm" in ova from the two-cell stage up to that of the blastula, and he regards it as establishing a structural continuity between the cell-elements, and forming an essential part of the organism. The achromatic perimorular zone shown in fig. 3 thus clearly corresponds to the ectoplasm described by Hammar in *Echinus miliaris*, and we consider it to be a vital constituent of the organism, and by no means the inert substance it is generally

FIG. 4.—Frog's ovum, showing an early stage in segmentation. The segmentation is incomplete, and the cell-elements at the "animal pole" are seen to be continuous with the deutoplasm of the "vegetative pole," in which the lines of cleavage are only just visible.

considered to be. It probably forms the medium through which one blastomere influences another during development.

It is a well-known fact that in centrolecithal ova, segmentation is incomplete, and it has been shown by Morin (22) that the daughter nuclei which at first lie in the middle of the ovum, subsequently migrate freely towards the surface along the radiating strands of the protoplasmic reticulum.

This direct structural continuity of the cell-elements of the morula mass appears to have been recognised by Wilson (33), who in his standard book on *The Cell* makes the following significant statement: "The unity of the embryo is not caused by a mere juxtaposition of the cells . . . this unity is physiological, and the facts point towards the conclusion that there must be a structural continuity from cell to cell, which is the medium of co-ordination." It follows that if this structural continuity be broken or

interrupted by mechanical displacement of the blastomeres, the unity of the organism is likewise broken up.

One of the most convincing proofs of the direct structural continuity of the blastomeres is shown by the following experiments. Roux (24), in an extensive series of articles covering the period between 1883 and 1903, elaborated a theory of development known as the germinal localisation theory of self-differentiation. According to this, certain portions of the ovum are early set apart for the formation of a definite organ or tissue of the embryo. The result of this idea is that by the time the morula stage is reached certain groups of cells are set aside for this purpose. It is evident, then, that according to this theory each of the two primary blastomeres ought to produce a hemi-embryo, and Roux at first considered that he had succeeded in producing from the blastomeres of frog's ova such a hemi-embryo, passing through the stages of hemi-morula, hemi-blastula, and hemi-gastrula.

Subsequent experiments by Wilson (33) and Morgan (21) on Amphioxus, and Jenkinson (16) on the frog, gave results diametrically opposed to those of Roux. They found that if the two primary blastomeres were completely separated from one another, each produced a *complete* embryo, though only *half the size* of the normal. Even a quarter blastomere was found to give rise to a normal blastula, gastrula, and sometimes even to the stage of an embryo, but only one-quarter the normal size. An eighth blastomere produced a morula, but this did not gastrulate. Finally, a one-sixteenth blastomere produced merely an irregular clump of cells. Further experiments by Driesch (7), Jenkinson (16), and others on the ova of Echinus gave almost identical results.

The conclusion one arrives at as a result of these foregoing experiments is, that if the two primary blastomeres did normally separate from one another completely, each ought *always* to give rise to a complete embryo in the natural process of development, but of course this is not so. The only inference, then, is that the continuity of the protoplasm of the two primary blastomeres is not completely severed, and this permits some mutual influence or interaction between the two, the result being a single complete embryo.

On studying later stages in the segmentation of the amphibian ovum, we discovered that the cyto-reticulum of the blastomeres could be traced through the cleavage planes as a direct connexion between the cell-elements. This appearance is rendered more striking by the fact that these strands cross the above-mentioned planes at right angles (fig. 5). We thus found a direct continuity in the morula stage which presumably must have resulted from a *division of nuclei in a mass of protoplasm*—

the whole constituting a *plasmodium*. The latter term is the only one which appears to us to meet the case, and we will therefore continue to employ it throughout this paper. It is certainly a more accurate title than syncytium, a term which suggests that the cell-elements were at one time separate and had become fused together secondarily. We hold, that protoplasmic continuity must have existed from the very first.

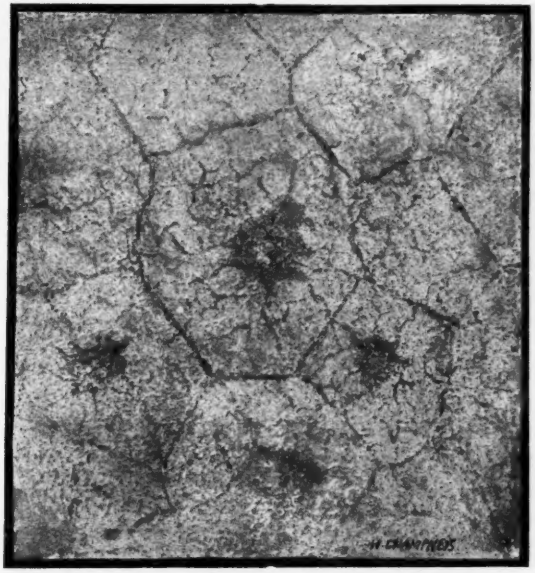


FIG. 5.—Later stage in the segmentation of a frog's ovum. The divisional planes between the cell-elements are now distinctly visible, and in the section appear as a protoplasmic network surrounding the cells, and characterised by a rich deposit of pigment granules. The cyto-reticulum of the enclosed cells is also pigmented, and its filaments will be seen to be continuous, not only with the pigmented planes of intercellular protoplasm, but also with the cyto-reticulum of neighbouring cell-elements.

The protoplasm of the blastodermic plasmodium can be conveniently divided into two kinds. That immediately surrounding the nuclei constitutes the endoplasm, and is of course readily recognisable. It is not so easy, however, to recognise the second kind, which we have decided (by contrast) to term the ectoplasm. The latter will be found not only to intervene between the cell-elements, but also to form a continuous zone surrounding the whole blastula mass. If this ectoplasmic layer increase in amount, the cell-elements become more or less completely separated; but

even then it still forms a connecting medium. At this point we wish to emphasise the importance of recognising this differentiation of the protoplasm of the blastula mass into a clear homogeneous ectoplasm and a perinuclear endoplasm; for we hope to be able to demonstrate subsequently a similar process of differentiation during the stages of development of practically all the tissues of the body, which will be found to constitute an

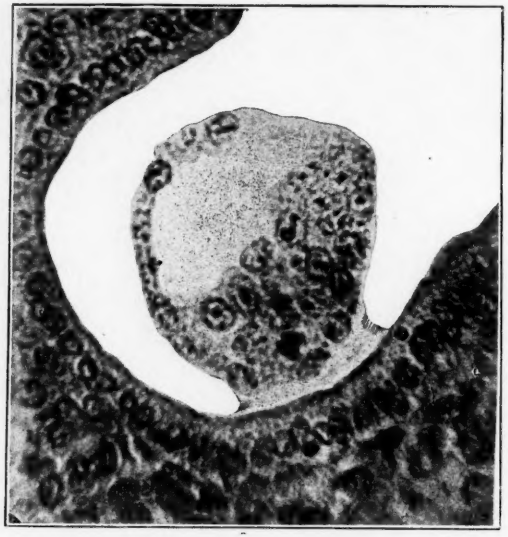


FIG. 6 is a microphotograph of a section through the free blastula of a mouse, which is at one part of its circumference becoming attached by fibrinous material to the uterine mucosa. The cell-elements are incompletely separated from one another. Some of the nuclei are undergoing karyokinesis and appear to be imbedded in a continuous protoplasmic matrix. The wall of the blastula must therefore be regarded as a "plasmodium," since the dividing nuclei are contained in a continuous matrix, and are not situated in separate "cells." From a specimen kindly lent by Professor Dendy. The section was stained with "picro-indigo-carmine."

important phase in their life-history. Thus, if one studies tissue-ontogeny from this new standpoint, one will be provided with remarkable evidences of the persistence of this primitive plasmodial condition even in the adult, the result of which, we venture to hope, will be a much more simplified conception of the histological structure of the body, than that provided by the cell theory, as usually understood.

In the blastula stage of mammals the separation of the cell-elements is also incomplete, and divisional lines are often absent altogether. Thus

fig. 6, which represents a critical stage in the development of the blastoderm of the mouse, simply shows a nucleated layer of protoplasm enclosing the

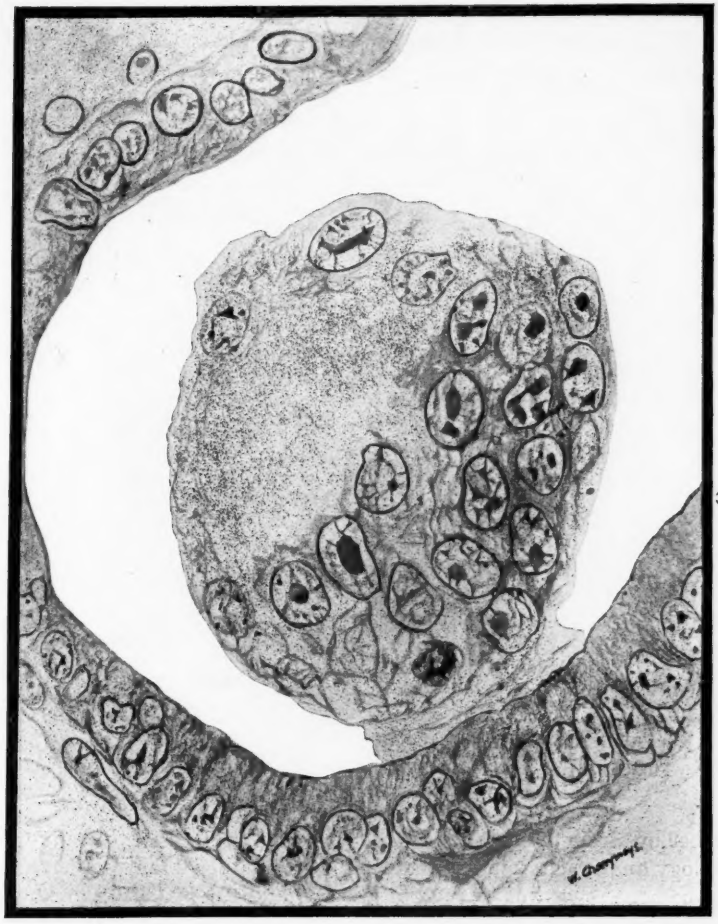


FIG. 7 is a higher-power view of the blastula shown in the previous figure in order to demonstrate its structure more clearly. Drawn under an $\frac{1}{8}$ apochromatic objective with compensating ocular $\times 7$.

cavity of the blastocyst, and constituting its wall. It will be observed that the outlines of the individual cell-elements, if visible at all, are only very

imperfectly shown, so that there is an obvious continuity of the protoplasm. The chromatin of some of the nuclei is in a disturbed condition (fig. 6), indicating that they are in one of the stages of karyokinesis. After studying this microphotograph one fails to recognise any resemblance to the conventional diagrams of the blastodermic vesicle which have been handed on from text-book to text-book. To represent cells sharply marked off from one

FIG. 8 is a low-power view of the entypy stage of a mouse embryo, which will be recognised in the centre of the microphotograph.

another by strongly marked boundary lines, is to give to students of embryology an inaccurate impression of the structure of the blastoderm, and it is to be hoped that this conventionality will soon be finally disposed of.

This continuity is well maintained in the entypy stage of the mouse embryo, as shown in figs. 8, 9, and 10. We have represented in fig. 10 a very highly magnified view of a group of the cell-elements shown in fig. 9. At first sight these appear to be mapped off from each other by divisional planes in the most definite manner. A more intimate examination clearly shows, however, that this appearance is due to the differentiation

of the protoplasm of the plasmodium into ectoplasm and nascent endoplasm. The latter forms the very definite zone immediately surrounding the nuclei, whilst the ectoplasm which at first sight appears to constitute the "partitions" between the individual cell-elements forms one continuous bond of union for the whole mass.

Take another example from a higher type of mammal. The plasmodial structure of the blastoderm has been very clearly represented by

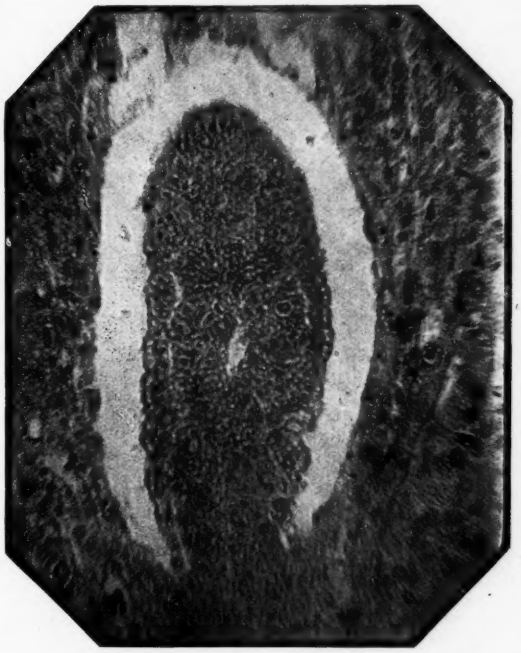


FIG. 9 is a high-power view of the entypy stage shown in fig. 8.

Hubrecht (15) in his well-known figure of the blastocyst of *Tarsius spectrum* (fig. 11). In this both the "formative cell mass" and the trophoblast appear to be a plasmodium. The fluid contained within the blastocyst seems to be a secretion from its plasmodial wall. The wall itself is represented as being mainly composed of a mass of protoplasm containing nuclei one of which is shown in the act of dividing. Here and there in the figure are cell-elements which have become mapped off in a greater or lesser degree from the general plasmodium.

In the blastocyst of the bat, as figured by van Beneden (1), the contained fluid appears first in the form of small vacuoles within the plasmodial mass. As these increase in size they coalesce to form the fluid filling the central cavity.

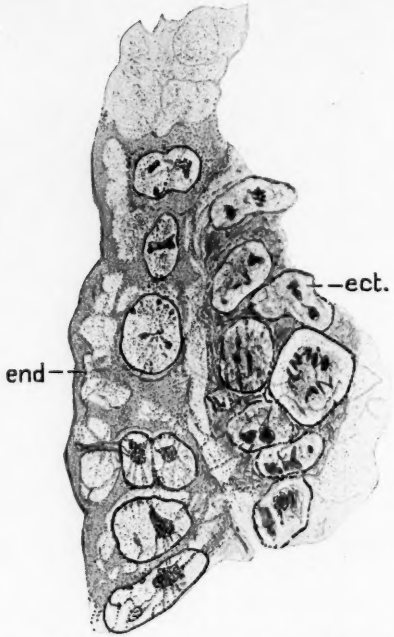


Fig. 10.—Portion of the endoderm and underlying ectoderm from the preceding specimen. The nuclei, some of which are undergoing mitosis, are seen to contain a clear nucleo-plasm. In the surrounding protoplasm is a similar clear material which appears to have been extruded in droplets from the nuclei, and sometimes forms a clear zone surrounding the nuclear membrane. This clear protoplasm we speak of as "endoplasm," and we believe it to be recently formed, *i.e.* in a *nascent* condition. The surrounding granular protoplasm is stained, and forms a continuous matrix. This granular protoplasm corresponds to the "ectoplasm," and it will be noted that where it forms a partition between adjacent nuclei, there is no indication of this partition consisting of two cell membranes lying in contact with one another, nor is there any indication of a space separating adjacent cell-elements. Drawn under an $\frac{1}{8}$ apochromatic objective with compensating ocular $\times 7$.

The relation of the two central cavities to the mesenchyme in the Teacher-Bryce (31) ovum also suggests that in the human subject the cavities of the blastocyst are formed within a plasmodium much in the same way as in lower mammals.

3. Continuity of the Ectoderm, Mesoderm, and Endoderm.

A study of the three-layered condition of the embryo shows that there still exists at this stage a direct continuity of the cell-elements. Those of the mesoderm usually exhibit a multipolar character, and it has been taught that this is due to an outward growth of processes from originally rounded cells which unite with those of neighbouring cells to form a network, or, in other words, a secondary continuity (fig. 12). A close examination of this stage of embryonic development shows, however, that these processes have been in direct continuity with one another from the very outset, the connecting strands of protoplasm being drawn out as a

Fig. 11 is a drawing of Hubrecht's well-known figure of the blastocyst of *Tarsius spectrum*. In this, both the formative cell-mass and the trophoblast appear to form a plasmodium.

result of the separation of the nuclei. Moreover, the processes of the mesodermic cell-elements lying next the ectoderm and endoderm are frequently seen to be in direct continuity with the protoplasm of these, and all three layers are distinctly continuous with one another at the primitive streak. Here also the cell-elements are imperfectly separated from one another, so that the actively growing tissue in this region must therefore be regarded as a plasmodium.

On tracing the ectoderm outward from the primitive streak the cell-elements certainly do appear to be marked off from one another by definite divisional planes. Upon closer examination, however, they are seen to be connected and held together by a thin ectoplasmic layer on the surface. This is most readily visible in the angles between the cell-elements, as in the entypy stage of the mouse embryo. It is probable that these elements are also connected with one another laterally, for they hold

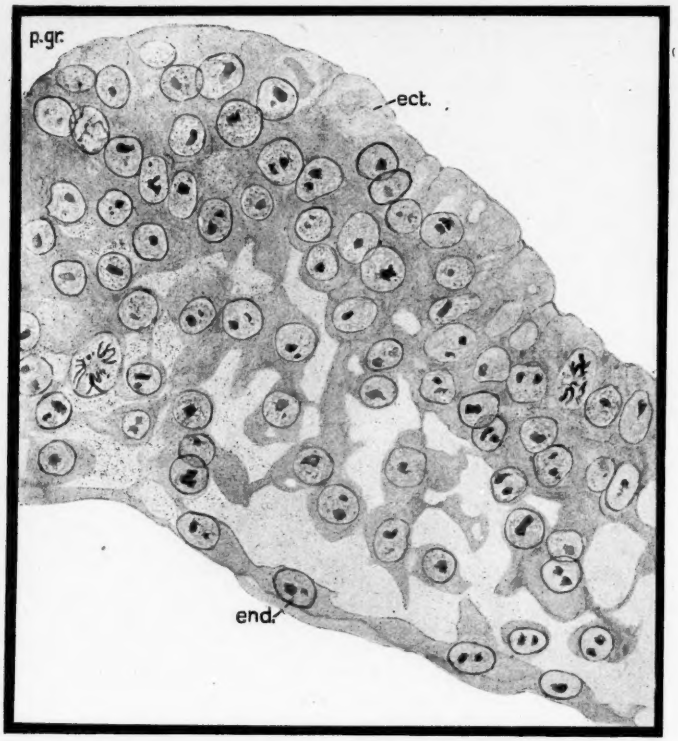


FIG. 12.—Transverse section through the primitive groove, and three primary layers of a chick embryo, incubated eighteen hours. The illustration shows one lip of the groove on the left-hand side; the ectoderm (*ect.*) is above, the endoderm (*end.*) below; between these two layers is the mesoderm, which consists of irregular strands of protoplasm connected by bridges of varying thickness, and containing nuclei, some of which exhibit karyokinetic figures. The cell-elements of the mesoderm are not only continuous with one another, but are continuous also with the ectoderm and endoderm. The continuity of the cell-elements of the mesoderm appears to be primary, for it will be noted that those nuclei which show mitotic figures (see nucleus to left in illustration) are situated in thickenings of the general reticulum, and are usually connected by protoplasmic bridges with several of the neighbouring nuclei. They do not appear to us to conform to the usual description, namely, that isolated cells of a rounded form wander out between the ectoderm and endoderm, and afterwards send out protoplasmic processes which join to form a reticulum. We seldom find isolated cells undergoing karyokinesis, either at the growing edge of the mesoderm or in any part of its extent between this and the primitive streak. Where such isolated cells are present, we believe that the protoplasmic bridges which have connected them with the neighbouring cell-elements from which they have originated have been broken in the preparation of the specimen, and the "cell" thus liberated has assumed a rounded form.

closely together, and are not separated by the action of the reagents employed for fixing the tissue, as they most certainly would be if the cells were merely in a condition of contiguity instead of organic continuity. One can thus trace this ectoplasmic bond of union from the early

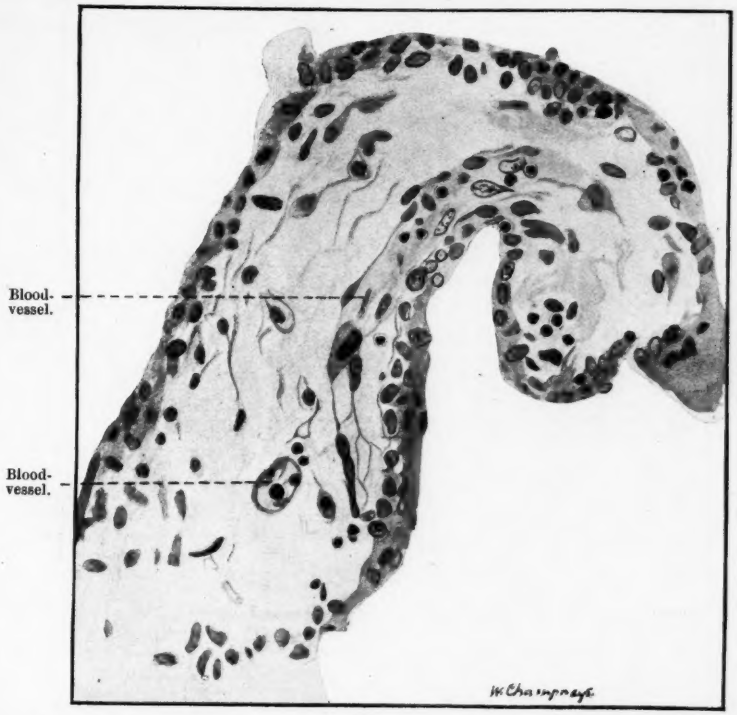


FIG. 13.—Section through a villus from the chorionic vesicle of a 9-mm. human embryo. The mesenchymatous core consists of a scanty meshwork of lightly stained protoplasm with nuclei at the nodes, and continuous externally with the granular protoplasm of the surface layers. The mesenchyme of the villus is also in direct continuity with the walls of the developing blood-vessels, one of which is shown cut transversely, the other longitudinally. Drawn with a $\frac{1}{8}$ objective.

developmental stages. Moreover, the intercellular material spoken of by histologists as inert "cement," and described by them as a secretion of the cells, we interpret as ectoplasm, and thus as an integral part of the living tissue.

The behaviour of the plasmodium during the three-layered stage exemplifies an interesting tendency it is constantly displaying, namely, the

surface cell-elements always arrange themselves in more or less definite layers, thus giving rise to the so-called ectoderm and entoderm. Another point which has impressed us strongly during these observations is, that the mesoderm is not produced wholly by a proliferation of the cell-elements in the region of the primitive streak, but also by a multiplication of the nuclei throughout the general plasmodial mass; that is to say, a generalised

FIG. 14.—A portion of the surface layer of the villus shown in fig. 13 drawn under an $\frac{1}{8}$ apochromatic objective with compensating ocular $\times 7$. The drawing shows an outer layer of oval, darkly stained nuclei, imbedded in a granular protoplasm. Next to this outer plasmodial stratum is "Langhans' layer," the nuclei of which are approximately spherical and less deeply stained. They are surrounded by a clear zone of unstained protoplasm similar in appearance to the clear nucleoplasm. This perinuclear protoplasm we speak of as *nascent endoplasm*, neighbouring zones of which are separated from one another by septa of granular stained protoplasm continuous externally with that of the outer layer, and internally with the mesenchymatous core. These septa at first give one the impression of separate cell-elements, but a closer examination shows that there is direct structural continuity throughout the specimen.

instead of an entirely localised proliferation. Fig. 12 exhibits this generalised multiplication of the nuclei during the three-layered stage.

4. Plasmodial Structure of a Placental Villus.

The central core of the villus (fig. 13) corresponds to the mesenchyme. It consists of a delicate protoplasmic network with nuclei at the nodes, and thus exhibits the typical plasmodial structure. The surface of the villus (shown highly magnified in fig. 14) exhibits the characteristic tendency referred to in the previous section towards a layering of the

cell-elements. Thus it shows an inner single stratum—the "absorptive layer of Langhans"—whilst the outermost coating permanently maintains its plasmodial character, constituting the "syncytium" of the chorionic villus. The plasmodial structure of this tissue has never been questioned, and has, in fact, been recognised for years. Still later, Langhans' layer merges with the syncytial coating of the villus, which then becomes spread out to form a single stratum of nucleated cell-elements connected at certain points with the protoplasm of the decidua basalis, and forming with it a

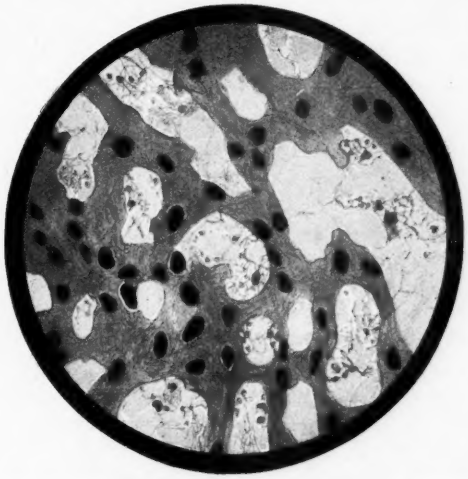


FIG. 15.—Section through the placenta of a 7-mm. guinea-pig embryo. The illustration shows part of a trabecula between two of the cotyledons. It consists of a plasmodial network, in the substance of which large oval nuclei are imbedded. Round each nucleus is a zone of lightly stained protoplasm, similar to the endoplasm surrounding the nuclei of Langhans' layer in the chorionic villi. Drawn under an $\frac{1}{6}$ apochromatic objective with compensating ocular ×7.

continuum. The core of the villus consists of the typical mesenchymatous network. In the trabeculæ of the meshwork are spaces which, as we hope to describe later, develop into the blood-vessels of the villus. Fig. 13 shows two of these primitive blood-vessels, one cut transversely, the other longitudinally. An examination of figs. 13 and 14 will show that the cell-elements covering the surface of the villus are in direct continuity with the mesenchymatous tissue of the core. The chorionic villus in all its features thus affords an instructive study of the structural continuity of developing tissue.

The maternal portion of the placenta likewise exhibits very strikingly

its plasmodial character. The tissue of the decidua basalis becomes greatly hypertrophied, and indeed *reverts* to its primitive plasmodial condition. Fig. 15 shows this characteristic tissue in process of being transformed into maternal blood sinuses.

5. Summary and Conclusions.

(1) In the developing blastoderm the nuclei with their contained chromatic material ought to be regarded as the structural units rather than the cell-elements as a whole.

(2) There is an organic continuity between the cell-elements of the developing blastoderm both in vertebrates and invertebrates. In the present paper we have traced this continuity up to the three-layered stage in mammals and in the chick embryo, in the chorionic villi and in the placenta.

(3) This continuity is in most cases primary, and not secondary (plasmodial rather than syncytial).

(4) Protoplasm may be differentiated into endoplasm and ectoplasm. The *nascent endoplasm* forms a clear, highly refractile zone immediately surrounding the nucleus. This merges into a more *mature endoplasm*, which in its turn undergoes transition into a granular *ectoplasm*.

(5) The nascent endoplasm, the more mature endoplasm, and the ectoplasm, represent three stages in the genesis of protoplasm. It is a well-recognised fact that the protoplasm of every living tissue has a limited period of activity during which its vitality is constantly being revived and rejuvenated by regulated supplies of nascent material. The latter is apparently a derivative of the nucleus, and is discharged from this in the form of *nascent endoplasm*. It would appear, therefore, that nutritive material ingested by the cytoplasm receives its final elaboration in the nucleus. From this standpoint we would argue further that the nascent endoplasm possesses the greatest activity, whilst the functions of the ectoplasm are more of a passive nature and are mainly in the direction of maintaining structural continuity between neighbouring cell-elements.

(6) The ectoplasm corresponds to the so-called intercellular substance, and forms an essential part of the continuous living tissue which with its contained nuclei constitutes a *plasmodium*.

REFERENCES TO LITERATURE.

(1) VAN BENEDEN, E., "Recherches sur les premiers stades du développement du Murin," *Anat. Anz.*, xvi., 1899.

(2) BERNARD, HENRY M., *Some Neglected Factors in Evolution*, G. P. Putnam and Sons, 1911. Also in *Quart. Journ. Micros. Science*, vols. xliii. to xlvii.

(3) BRÜCKE, C., "Die Elementarorganismen," *Wiener Sitzber.*, xliv., 1861.

(4) CAMERON, J., *Journ. of Anat.*, 1905.

(5) CAMERON, J., *Journ. of Anat.*, 1912.

(6) CAMERON, J., *Brain*, 1906.

(7) DRIESCH, H., *Arch. Ent. Mech.*, x., 1900, and xvi., 1903.

(8) FLEMMING, W., *Zellsubstanz, Kern, u. Zelltheilung*, Leipzig, 1882.

(9) GODLEWSKI, *Archiv f. Mikro-Anat.*, Bd. lx., 1902.

(10) HAMMAR, J. A., "Ueber eine allgemein vorkommende primäre Protoplasma verbindung zwischen den Blastomeren," *Arch. f. Mikro-Anat.*, Upsala, xlvii. p. 14, and xlix.

(11) HARDESTY, J., *Amer. Journ. of Anat.*, vol. iii., 1904.

(12) HEAPE, W., *Quart. Journ. Micros. Sci.*, vol. xxiii., 1883.

(13) HEITZMANN, J., *Sitz. d. k. Akad. Wiss. Wien*, xlvii.

(14) HIS, WILHELM, "Ueber Syncytien, Epithelien, u. Endothelien," *Verh. Ges. d Natf. Leipzig*, LXXII., ii. 2, 1901 (273–276).

(15) HUBRECHT, A. A. W., *Verhand. d. Koninklijke Akad. van Wetterschappen te Amsterdam*, viii., 1902.

(16) JENKINSON, J. W., *Experimental Embryology*, 1909.

(17) KERR, GRAHAM, *Trans. Roy. Soc. Edin.*, vol. xli., Part I.

(18) LILLIE, F. R., *Development of the Chick*, 1908, pp. 38–52.

(19) M'BRIDE, E. W., *Text-book of Embryology*, vol. i., 1914.

(20) M'GILL, CAROLINE, *Internat. Monatsschrift. Anat. u. Physiol.*, Bd. xxiv., 1907.

(21) MORGAN, T. H., *Anat. Anz.*, x., 1895, and *Arch. Ent. Mech.*, xix., 1905.

(22) MORIN, *Development of Astacus*, Korschelt & Heider.

(23) RETZIUS, G., "Die Intercellularbrücken des Eierstockeies, und der Follikelzellen," *Verh. Anat. Ges.*, 1889.

(24) ROUX, W., *Virchow's Archiv*, 1889.

(25) SCHLEIDEN, M. J., "Beiträge zur Phytogenesis," *Müller's Archiv*, 1838.

(26) SCHULTZE, F. E., *Sitzungsberichte der Kön. Pr. Akad. der Wissenschaften zu Berlin*, 1896.

(27) SCHWANN, TH., *Mikros. Untersuch. über die Uebereinstimmung in der Struktur und dem Wachstum der Tiere und Pflanzen*, Berlin, 1839.

(28) SEDGWICK, ADAM, "On the Inadequacy of the Cellular Theory of Development," *Quart. Journ. Micros. Sci.*, xxxvii.

(29) SPALTEHOLZ, W., *Verhandl. Anat. Gesellsch.*, Rostock, 1906.

(30) STUDINCKA, F. K., *Sitz. der k. böhm. Ges. der Wiss. in Prag*, 1897.

—— "Ueber Stachzellen und sternförmige Zellen in Epithelien," *Sitz. der k. böhm. Ges. der Wiss. in Prag*, 1902.

(31) TEACHER and BRYCE, *The Early Development and Imbedding of the Human Ovum*, Glasgow, 1908.

(32) WEISMANN, A., *The Germ Plasm*, transl. by W. N. Parker, 1893.

(33) WILSON, E. B., *The Cell in Development and Inheritance*, 1906, pp. 58–61.

TWO EXAMPLES OF CARDIAC MALFORMATION.

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CONGENITAL malformations of the heart usually receive scant notice in standard medical works. This is true not only of general text-books on medicine, but also of works specially devoted to affections of the heart.

Such inadequate treatment of an important subject may perhaps be explained on the assumption that these congenital malformations are frequently regarded as mere curiosities of development; and since the more pronounced examples are often incompatible with life, they are also regarded as of no clinical importance.

Some of these cases of defective cardiac development are, however, quite compatible with life. They are, moreover, sufficiently common to render their recognition essential to the general practitioner; but a clear description of their anatomy, combined with an account of their symptomology and of the physical signs they produce, is yet to be written.

A mere glance at the specimens of congenital abnormality of the heart which may be seen ranged on the shelves of any well-equipped anatomical museum is sufficient to show that quite a large proportion were taken from adults, or from children who had passed well beyond the age of infancy. Of the two specimens which we shall describe, one was taken from a woman who had reached the age of fifty.

Now, all cases of congenital malformation of the heart do not of course present an identical clinical picture, but the symptoms will vary with the nature of the malformation and with the degree of interference with the normal circulation. For example, in some cases there is defective development of the right ventricle and pulmonary artery; and in these cases the lungs will receive a diminished and perhaps inadequate supply of blood. In others (*e.g.* one of the cases which we shall describe) it is the left ventricle and the aorta which are ill-formed, with compensatory enlargement of the right ventricle and pulmonary artery; and in these cases, while the lungs receive an ample supply of blood, the body generally, including the brain, receives a deficient supply, the blood entering the aorta through a patent "ductus arteriosus."

It will, moreover, be obvious that to relieve the various symptoms which are produced by the several types of congenital malformation of the heart different treatment must be employed, and more especially so according as the pulmonary or systemic circulation is chiefly affected. It is of the greatest importance therefore that the signs and symptoms produced by these different types of cardiac malformation should be carefully studied in all cases, and recorded, so that an opportunity will be afforded of comparing one case with another, and of diagnosing the kind of abnormality during life.

Classification on an anatomical basis of the different kinds of defective cardiac development has now been satisfactorily accomplished, and the results have been published by Keith and other writers. In order to complete our knowledge of these cases, however, it remains for clinicians to correlate the signs and symptoms which these different malformations of the heart produce. It will then be possible to recognise the type of malformation during the patient's lifetime, and to carry out the treatment of individual patients upon a rational basis.

There is one other point which we feel it necessary to emphasise before describing these two specimens, namely, that in a very large number of cases of cardiac abnormality which are brought to anatomists from the "post-mortem" room, the heart has been cut away close to the origin of the large blood-vessels, and sometimes, even, a large portion of the walls of the auricles and the pulmonary veins have been cut away. Under these circumstances, it is often difficult and sometimes impossible to say how the circulation has been carried on. In all cases, therefore, in which some congenital malformation is suspected, the relations of the large vessels should be noted before the heart is opened, and when the heart is removed, the arch of the aorta, a considerable length of the venæ cavæ, and all the pulmonary vessels (arteries and veins) should be removed with the heart.

Case I.

Congenital Malformation of the Left Ventricle and Ascending Aorta.

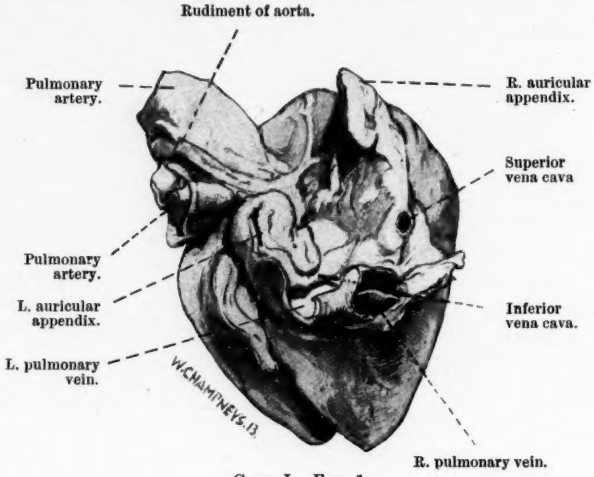
This case occurred in the practice of Dr T. G. Wilson of Adelaide, South Australia, to whom we are indebted for the specimen. The infant became cyanosed soon after the cessation of the placental circulation, and it died forty-eight hours after birth.

The specimen may be described as a three-chambered fœtal heart, consisting of right and left auricles, and right ventricle; the left ventricle and ascending aorta being quite rudimentary and functionless.

The external appearance of the heart when viewed from above and

behind is represented in fig. 1. The drawing shows the rudimentary ascending aorta coursing upward behind the pulmonary artery and right auricular appendix. A small left coronary artery is also present which passes down between the left auricular appendix and pulmonary artery, and indicates the position of the anterior interventricular groove. The ascending aorta above the origin of the coronary arteries is quite impervious.

Fig. 2 shows the cavity of the left auricle (L.Ar.) viewed from behind. The drawing also shows the interauricular septum (S.Pr.), and widely open foramen ovale. A minute recess which represents the cavity of the rudi-



CASE I., FIG. 1.

mentary left ventricle, and which is situated in the position of the mitral orifice, will also be recognised.

In fig. 3 the heart is represented as seen from in front, the right ventricle and pulmonary artery having been opened. The tricuspid orifice, the infundibulum, and the semilunar valves of the pulmonary artery will be readily recognised.

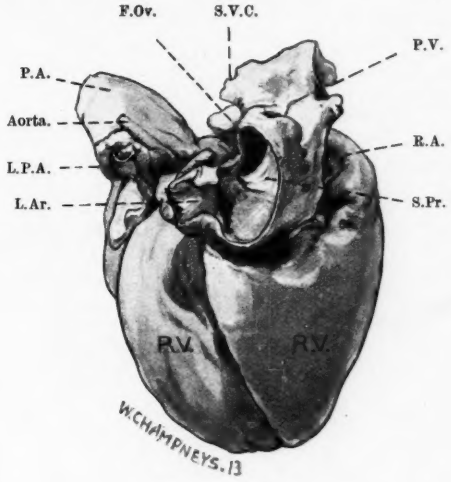
The large blood-vessels at the base of the heart were cut off close to their origin and termination. If these had been preserved we should probably have found an open "ductus arteriosus," through which the blood coming from the right ventricle and pulmonary artery would have reached the arch of the aorta, beyond the imperfectly developed and impervious ascending portion.

Similar cases of suppression or incomplete development of the left

ventricle and ascending aorta have been described by Professor Arthur Keith and Dr Eric Gardner, specimen 616.7, Museum, R.C.S., Eng. They have to be distinguished—

(1) From three-chambered hearts in which the *right ventricle and pulmonary artery are rudimentary or absent.*

In these, owing to the absence or diminutive size of the right ventricle, and of the impossibility of the blood escaping from the right auricle through the tricuspid orifice, the right auricle empties itself through a widely-open foramen ovale directly into the left auricle and so into the left ventricle



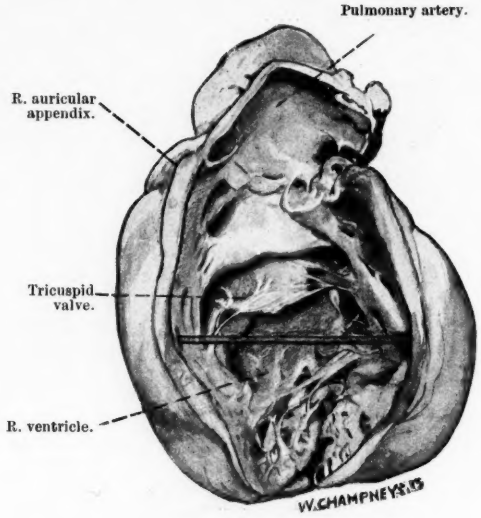
Case I., Fig. 2.

and aorta. Part of this blood finally also reaches the lungs from the aorta by means of a patent "ductus arteriosus" in which the blood courses in the reverse direction to the normal. The blood may, however, reach the pulmonary artery by a different route, as in a case of Dr F. S. Mackenzie, described by Professor Arthur Keith. In this heart the body of the right ventricle was rudimentary, but the infundibular or bulbar portion and the pulmonary artery were present. In this case the blood reached the pulmonary artery from the left ventricle by passing successively through a patent interventricular foramen, a narrow ostium bulbi, and the bulb or infundibulum. During life venous and arterial blood would have mixed in the left auricle, the former entering through the foramen ovale, the latter entering from the pulmonary veins.

(2) They have to be distinguished from that form of three-chambered heart in which there is a failure in the separation of the right from the left ventricle, owing to the *absence of an interventricular septum.*

In these cases both right and left auriculo-ventricular orifices are present, and open into a single common chamber, from which two large blood-vessels emerge, the pulmonary artery and the aorta.

An interesting example of this defect was described by the late Professor A. H. Young, in the *Journ. Anat. and Physiol.*, vol. xli., 1907. It occurred in a man "who during the greater part of his life appeared fairly healthy,



Case I., Fig. 3.

and any malformation of the heart was not even suspected." He lived to the age of thirty-five, and was not cyanosed until shortly before his death.

In all these types of three-chambered heart there will be a mixture of venous with arterial blood. In the case which we have described, assuming that the "ductus arteriosus" was patent, and that the pulmonary circulation had been established, the arterial blood coming from the lungs through the pulmonary veins on entering the left auricle was unable to pass by the usual route through the mitral orifice, and it must therefore have passed from left to right through the patent foramen ovale into the right auricle, where it mingled with the venous blood entering this chamber from the superior and inferior venæ cavæ. The mixed arterial and venous blood

then passed through the tricuspid orifice into the right ventricle, and discharged into the pulmonary artery. It reached the lungs by the right and left branches of this vessel, and the body generally by means of the patent "ductus arteriosus" and aorta.

The chief indications of the condition were cyanosis, dyspnœa, and the signs of a defective systemic circulation.

Case II.

A Heart showing a Constriction in the Position of the Ostium Bulbi, associated with a Persistent Interventricular Foramen.

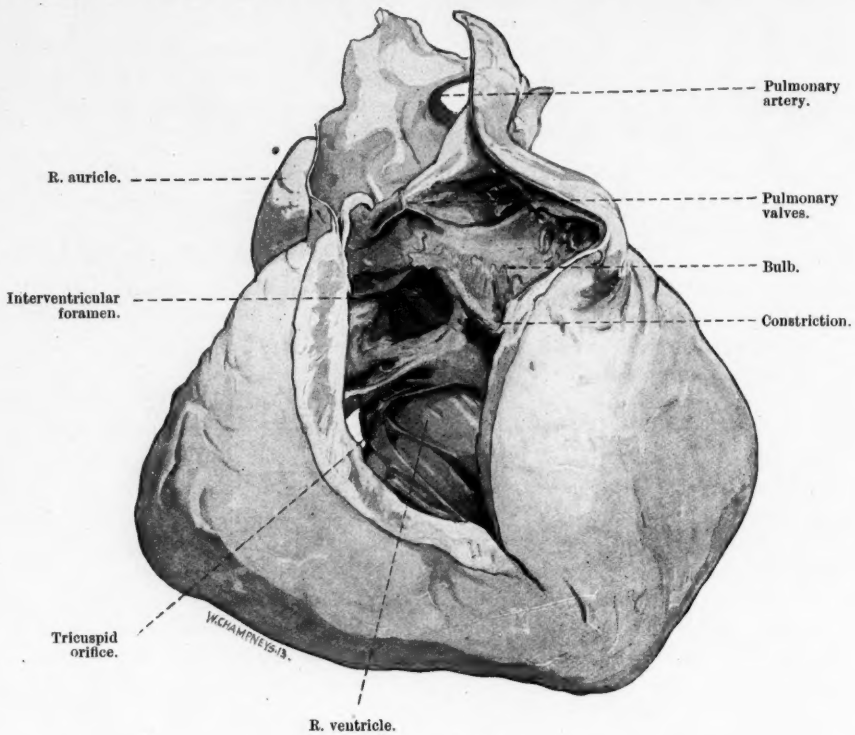
This specimen was obtained from a woman who had attained the age of not less than fifty years. The patient was a chronic invalid, and she had been under the care of many medical practitioners, some of whom were experienced clinicians. Yet notwithstanding this fact, the existence of the cardiac malformation was not diagnosed during life. On the other hand, the patient was thought to be suffering from chronic pulmonary tuberculosis, a view which was shown at the autopsy to have been entirely erroneous.

The heart in this case appears to be an example of an imperfect development of that part of the right ventricle which corresponds to the "bulbus arteriosus" of fishes. The right ventricle, the walls of which are greatly hypertrophied, is subdivided by a collar-like constriction into a small upper chamber, viz. the bulb or infundibulum, and a large lower chamber corresponding to the body of the ventricle (fig. 1). The opening between these two chambers (ostium bulbi) would just admit the point of a finger. The interventricular foramen will be seen to lie behind and below the constriction, so that the blood contained in the body of the ventricle would be discharged partly into the aorta through the interventricular foramen, and partly into the pulmonary artery through the ostium bulbi. It will be noticed also that the pulmonary semilunar valves are much thickened and deformed by endocarditis, and that the interior of the bulbous portion of the ventricle is rough and granular. Attached to the posterior semilunar valve is a large pedunculated vegetation.

Fig. 2 shows the heart opened from behind, and the cavity of the left ventricle held open by a glass rod. The interventricular foramen will be observed below the anterior and right posterior semilunar valves of the aortic orifice. The foramen is bounded below by a thick rounded border, which is roughened by endocarditis, and continuous on the right side of the septum (fig. 1) with the anterior papillary muscle of the tricuspid valve.

The pulmonary artery is thin-walled and considerably smaller than the aorta. In the removal of the heart the aorta was severed at the junction

of its ascending part with the arch, and the pulmonary arteries were cut just beyond the bifurcation of the main vessel, so that the "ligamentum arteriosum," or the "ductus arteriosus" if this vessel had remained open, was not preserved. It is probable, however, that sufficient blood would have entered the pulmonary artery to maintain the pulmonary circulation,

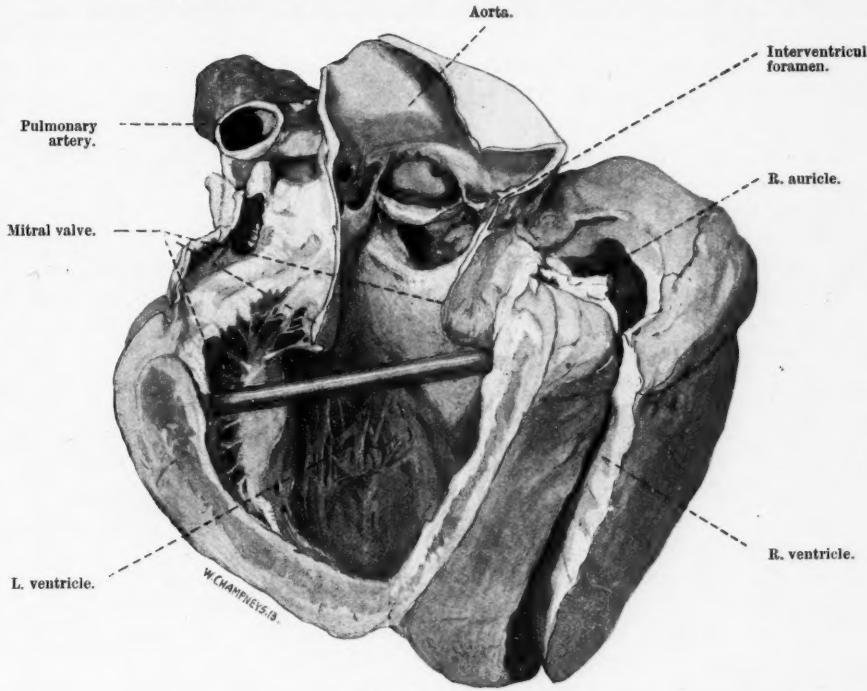


CASE II., FIG. 1.

without the "ductus arteriosus" remaining patent. In cases, however, of more complete arrest and those in which the pulmonary artery is absent or impervious, the "ductus arteriosus" persists. (According to Keith, in about 37 per cent. of all cases.) The blood-supply of the lungs in these cases is thus derived from the aorta, and the direction of the current in the "ductus arteriosus" through which the blood reaches the right and left pulmonary arteries is reversed.

In the remaining cases, if the child has survived its birth, and the

"ductus arteriosus" is closed, the lungs receive their blood from the bronchial arteries, and from the accessory branches of the intercostal and pericardio-phrenic arteries. (O.T. Arteria comes nervi phrenici.) These arteries undergo a remarkable enlargement, and they are also increased in number. Thus the existing bronchial circulation is made use of to perform



CASE II., FIG. 2.

the function of the pulmonary vessels, and in addition to this new channels are opened up which do not normally exist.

The circulation thus developed is feeble, but it suffices to maintain life.

The presence of endocarditis affecting the "bulb" and the pulmonary semilunar valves is of considerable interest. It has been supposed that in similar cases in which unmistakable signs of a previous inflammation of the endocardium have been present, the endocarditis occurred during the early stages of fœtal life, and has given rise to a cicatricial constriction, and further that the interventricular foramen, so commonly present in these cases, persists for the escape of blood whose passage through the

narrow infundibulum and pulmonary artery is restricted if not arrested. According to Schipmann, the most common and important effect of intra-uterine endocarditis is stenosis of the pulmonary orifice, and he also states that the limitation of the endocarditis to the right side of the organ during intra-uterine life comes under the same law as its limitation to the left side in extra-uterine life. In both cases it is the cavity which has most work to perform that is affected. According to this view, cases in which the interventricular foramen has not persisted are produced by endocarditis occurring after the period when this foramen is normally closed. The closure is effected by the fusion of the interventricular septum with the bulbar septum, and this takes place in embryos between 12 mm and 18 mm. in length, and at the age of six to seven weeks. It is probable, however, that the endocarditis is a secondary incident which has occurred after birth, and that the primary condition is constriction. It is probable also that the constriction is attributable to a primary defect in development rather than to a fœtal endocarditis; for if fœtal endocarditis were the cause, we should expect also to find stenosis of the right auriculo-ventricular orifice with endocarditis of the tricuspid valve, but this is not found, on the contrary congenital stenosis of the right auriculo-ventricular orifice is extremely rare. Fœtal endocarditis, moreover, does not explain those cases in which there is complete obliteration of the pulmonary artery extending as far as its bifurcation, and associated with a failure in the expansion of the infundibular or bulbar portion of the right ventricle, such as is present in a specimen described and figured by Professor Keith in the *Lancet* of August 7, 1909, p. 361.

The persistence of the interventricular foramen is apparently secondary to failure in expansion of the bulbar portion of the right ventricle, and its presence, and size when present, depend largely upon the extent of the defect.

Cases of imperfect development of the bulbous portion of the right ventricle, or of constriction between this part and the body of the ventricle, are not uncommon. Two specimens were described and figured by Dr Thomas B. Peacock in his work on *Malformations of the Heart*, in 1866. In one of these taken from a child aged five there was a septum in the right ventricle, producing a marked division between the sinus and the infundibular portion, *the heart being otherwise well formed.* In the second case there was a partition between the two portions of the right ventricle, with *deficiency of the interventricular septum*, and a narrow pulmonary orifice.

The first case is of importance as it demonstrates that a defective development of the "bulb" may exist without an interventricular foramen;

and therefore that the small size of the "bulb" and pulmonary artery are not a secondary result of the diminished amount of blood flowing through these parts, owing to the escape of blood through an interventricular foramen into the aorta. Their small size is due to an arrest of the normal developmental expansion of these parts—this being the primary defect, and the persistence of the interventricular foramen secondary.

Summary.

The first case is an example of a three-chambered heart.

There are three possible varieties of the three-chambered heart:—

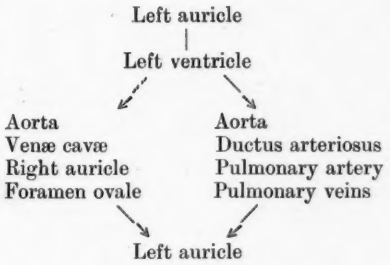
(1) The two ventricles are merged into a single common chamber, the interventricular septum being absent.

In this variety the circulation is altered only to the extent that arterial and venous blood mix in the common ventricle, and a portion of venous blood fails to pass through the lung and consequently remains unoxygenated.

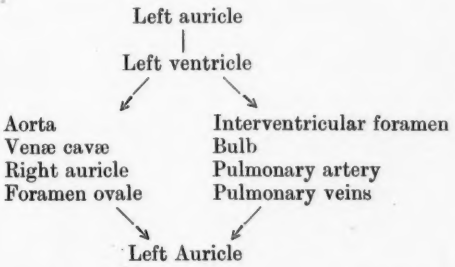
(2) The right ventricle is rudimentary or absent, and the three-chambered heart consists of right and left auricle and a left ventricle.

The circulation is completed by either one or other of the following paths:—

(A)

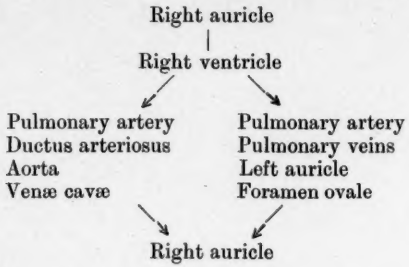


(B)



(3) The left ventricle is rudimentary or absent, and the three-chambered

heart consists of a right and left auricle and a right ventricle. (Such a case is described in the text.) The circulation is completed as follows:—



In each of these last two varieties the lung receives its blood-supply by a collateral circulation as it were, and therefore, as in the first variety, part of the blood remains unoxygenated.

The second case is that of a heart showing a constriction in the position of the ostium bulbi, associated with a persistent interventricular foramen.

That portion of the right ventricle known as the "bulb" or "infundibulum" is imperfectly developed, leading in effect to a pulmonary stenosis. The right ventricle is consequently hypertrophied and the interventricular foramen persists.

The bulb and the pulmonary semilunar valves are affected with endocarditis, and the hypothesis is considered that the endocarditis is an antenatal phenomenon, and is in fact the "fons et origo" of the cardiac malformation, viz., constriction of the ostium bulbi with consequent patency of the interventricular foramen.

But while the view is accepted that the closure of the interventricular foramen is prevented by the unequal distribution of pressure in the two ventricles, there is ample evidence to show that endocarditis is not the primary cause of the bulbar constriction, which may, in fact, occur in the absence of any inflammatory change whatever.

THE THYROIDEA IMA ARTERY.

By G. Wyatt Pratt, B.A.,
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Introduction.

This artery, which is described in all the anatomical text-books, may arise from the arch of the aorta (arcus aortæ), from the innominate artery (a. anonyma), from the right common carotid (a. car. com. dext.), from the right or left subclavian, and in rare cases from one of the branches of the subclavians. It varies in diameter from ·5 mm. to 3 mm., and it may consist only of a single trunk or of multiple bifurcations and terminal arborisations. In short, there does not seem to be any cogent reason for cataloguing, or even for naming, this aberrant thyroid artery. Unfortunately, an element of associative importance appears—the artery is of importance surgically in the operation of tracheotomy.

Recognition of the Thyroidea ima Artery.

Neubauer (1) recognised the thyroidea ima, and after him it was called *the thyroid artery of Neubauer*. Sappey (2) notes that the thyroidea ima is a supernumerary inferior thyroid, that it springs from the innominate arch, and adds that it has been very rarely observed. Beaumanoir (3) states that he has seen cases in which, with all the thyroid arteries of a normal size, the thyroidea ima was of a large calibre and divided into three branches, the upper two ascending and taking up their positions, the one lateral to the trachea, the other lying in the middle line and terminating in ramifications and anastomoses with the other thyroid arteries in the thyroid gland. The descending branch divided into two twigs, the ascending one passing upwards to terminate in the thyroid gland, while the other descending limb passed downwards to the region of the aortic arch and terminated in the surrounding tissue.

He noticed also in another case (4) the origin of the thyroidea ima from the innominate artery, in the form of a branch of 2 mm. in diameter which terminated in the sterno-thyroid muscles and subjacent tissue, and had no connexion whatever with the thyroid gland.

Taylor and Grell (5) described a case in which, associated with the origin of an inferior thyroid artery of normal calibre, a small thyroidea

ima was evolved from the innominate artery. Testut (6) states that the thyroidea ima may spring either from the arch of the aorta or from the innominate artery. He goes on to state that its presence is solely connected with the lack of a sufficient blood-supply for the thyroid gland from its normal sources.

Theile (7) remarked that the thyroidea ima was either a displacement or a reduplication of the inferior thyroid artery. Macalister (8) states that a *middle thyroid artery* is sometimes seen to rise from the innominate artery and ascend on the trachea to supply the thyroid gland.

Deaver (9), Morris (10), and Young and Robinson (11) all state that the thyroidea ima is given off by the innominate artery, and that its sole object is the arterial supply of the thyroid body. M'Murrich (12) lays down the definite precept that the presence of the thyroidea ima is "associated with a more or less extensive reduction of the size of one or other of the thyroid arteries."

In my own experience I have found the thyroidea in two subjects only during three years. In the first case the artery came off from the right common carotid at a distance of one inch below the bifurcation and passed first inwards, and then directly upwards for a short space, when it divided into four trunks, all of which terminated, after supplying the thyroid gland, in anastomoses with the arteries proper of the thyroid body. The artery was of substantial calibre, and there was no diminution either in diameter or in number of the normal thyroid arteries. The thyroid body also was of the usual dimensions. In the second case the thyroidea ima came off as a short twig from the right common carotid artery inferior to the bifurcation. Its course was practically coincident with that of the inferior thyroid artery, and terminated in the thyroid body.

Discussion and Conclusions.

In the face of such a conflicting mass of evidence, it would at first sight appear difficult to formulate any definite explanation of the appearance and significance of the thyroidea ima.

It is impossible to agree with M'Murrich in the assumption that the thyroidea ima is only developed when there is insufficiency of blood supply — either by congenital or acquired conditions — to the thyroid body. Unfortunately for this view, there are many cases on record where the thyroidea ima has been observed to have no connexion with the thyroid body at all. It is noticeable, however, that whenever these descending branches are present they are slender and invariably pass downwards towards the locality of the thymus gland. This would account for the

usual extreme slenderness of the thyroidea ima when it arises from the arch of the aorta or the lower part of the innominate. In all recorded cases it is noticeable that the thyroidea ima when present—either as a single branch not proceeding to the thyroid body, or as a twig passing to the thyroid gland and evolving another offshoot coursing away in the direction of the thymus—is universally of diminutive calibre. When the thyroidea ima is devoted solely to the thyroid body, it is either a single or multiple artery of large calibre. It may be associated with diminutive development of the thyroid arteries, or, on the other hand, they may be normal. There does not seem to be any hard-and-fast rule. In the higher Primates, Keith (13) found on dissecting one gorilla, four gibbons, three semnopitheques, and two macaques that in some of the last two genera the thyroidea ima arose from the carotid artery in the neck, while in the other cases it arose from the aortic arch. From these facts it would seem that the thyroidea ima is just as variable in the higher Primates as it is in man, and that it has no definite position which can be made a precept.

In reviewing the facts at my disposal, I find the following singular agreement. When the thyroidea ima is given off from any artery in the region of the neck, it is usually of a noticeable diameter; when it is given off from an artery which is not in the neck, it is invariably of slender calibre. Against this must be set the fact that when a "neck" thyroidea ima artery gives off a branch which descends towards the thymus, it is always of slender dimensions. The reason for this is not far to seek. The thyroidea ima when passing to the thymus is of very small size simply and solely because the body to which it had formerly directed its supply has more or less completely atrophied as a gland. It may be questioned from this why the thyroidea ima has not altogether atrophied, considering that its purpose in life has gone. This is easily answered. Waldeyer has shown that total degeneration of the thymus never occurs, and that throughout life it retains something of its old form. In this thymic connexion it would be better not to call the artery thyroidea ima, but *thymica accessoria*, thus giving the artery its proper significance. When the thyroidea ima is of large size, and passing to the thyroid body, its presence may be due to one of two causes: (*a*) the absence or malformation of one or more of the superior or inferior thyroid arteries due to defective development of the thyroid arteries proper, or (*b*) the necessity of a large blood-supply to the thyroid gland from physiological or pathological causes.

It will be seen that this artery (whether in the position which justifies the name of thymica accessoria, or in the position in which it should be

called thyroidea ima) is purely an anomalous and abnormal condition, and does not justify its presence in anatomical nomenclature at all. M'Murrich (12) and Thane (14) state that the thyroidea ima is present in 10 per cent. of bodies, but this figure would appear to be much exaggerated.

REFERENCES.

(1) Neubauer, *Op. Anatom. collecta*, 1786.
(2) Sappey, *Traité d'Anatomie*, 1869.
(3) Beaumanoir, *Bull. de la Soc. Anat.*, tome vii., 4e sér., 316, 1882.
(4) Beaumanoir, *ibidem*, 317, 1882.
(5) Taylor and Grell, *Jour. of Anat. and Phys.*, vol. xxxvi. 288, 1902.
(6) Testut, *Traité d'Anatomie Humaine*, tome 2me, 151, 1900.
(7) Theile, *ibidem*, 151.
(8) Macalister, *Human Anatomy*, 631, 1890.
(9) Deaver, *Surgical Anatomy*, vol. ii. 126, 1900.
(10) Morris, *Human Anatomy*, 533, 1915.
(11) Young and Robinson, *Cunningham's Text-book of Anatomy*, 888, 1913.
(12) M'Murrich, Piersol's *Human Anatomy*, 729, 1907.
(13) Keith, *Jour. of Anat. and Phys.*, vol. xxix. 455, 1895.
(14) Thane, *Quain's Elements*, vol. ii. 388.

THE WEST SCOTTISH SKULL. By Thomas H. Bryce, M.D.,

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In the anatomical department of the University of Glasgow we possess a great series of skulls all obtained from one site. They were obtained during the removal of an old graveyard, thanks to the zeal of Dr W. H. Hutton, now Lecturer in Anatomy at Queen Margaret College. It was his intention to have worked over the collection, but from circumstances beyond his control he was unable to carry this out. Accordingly, it was arranged that Dr Matthew Young, the Senior Demonstrator, who has an aptitude for this class of work and a sufficient knowledge of statistical methods, should undertake the task. The work has occupied a number of years, and the results have now been published in the *Transactions of the Royal Society of Edinburgh*, by aid of a grant from the Carnegie Trust. As Dr Young desired to present the work as a Thesis for the degree of Doctor of Medicine, publication of the individual sections of the work has been reserved, and the whole is now presented as a complete and intensive study of the brain case from every point of view, statistical and morphological. The research in its progress has had special interest for myself, and I think the memoir of sufficient importance to warrant the presentation of a general account of the main results for the benefit of those who have not the leisure to work over the great mass of detail included in it.

When one first saw the whole series laid out on the floor preparatory to a general classification of the individual specimens, one was forcibly struck with the uniform character of the skulls. Apart from variations in size, only one type seemed to be represented, and that obviously a dolichocephalic type or one in the lower register of the mesaticephalic class.

It was at once borne in on one that an almost unique opportunity presented itself for a biometrical study of the variability and correlations of the skull. It was discovered in due course that the series satisfied Karl Pearson's test for homogeneity, the standard deviation for length being 5·94 and that for breadth 4·76; further, that the mean cephalic index for male skulls was 74·41 and for female 76·03.

Here then was a long and homogeneous series of dolichocephalic type which would yield means approaching morphological actualities. From

the papers and atlases of Berry and his co-workers in Australia there are now available data for obtaining true means for Tasmanian and Australian skulls. The main interest of the research on the morphological side came, therefore, to centre in the detailed comparison of two dolichocephalic types, the one on a high the other on a low plane of civilisation, and in the determination of the factors involved in the growth and expansion of the bony capsule in this type of cranium as the brain increased in size.

The total number of skulls left, after all juvenile and about 50 metopic skulls were eliminated, was three short of 600. These were divided into three classes: (*a*) male skulls, (*b*) female skulls, and (*c*) skulls of doubtful sex. 405 skulls were found in class (*a*), 100 in class (*b*), and the remainder in the doubtful class. These last were eliminated from the research, although the measurements are included in the appendix to the memoir. Of the 405 male skulls 100 were selected for special morphological analysis, and they were ultimately divided in the sagittal plane for estimation of the spheno-ethmoidal and other angles.

The large proportion of male to female skulls may raise a doubt as to the correctness of the identification of sex, which is of course notoriously difficult in many cases. It is possible that most of the doubtful skulls should have been classed as female, but the correctness of the classification is supported by the fact that there is no great difference in the means in the complete male group and the more stringently selected group of 100 male skulls, in which the male characteristics were specially well marked. It is clear, however, that in making this selection the larger skulls were unconsciously chosen, as the mean capacity of the group is 50 c.c. in excess of that of the whole male series.

The first section of the memoir embodies a comparison by ordinary craniological methods of the West Scottish with Sir William Turner's series of Scottish skulls. It was found that although in all essential particulars the West Scottish skulls were identical in their characters with Turner's Renfrewshire group, the series differed from his complete series in having a distinctly lower mean width. In short, the brachycephalic element which Sir William Turner showed to exist in appreciable numbers in the population of Scotland is practically absent in our collection.

While 20 per cent. of Turner's skulls had an index of 80 and upwards, only 3·7 per cent. of our 505 skulls had indices rising to that level. Further, 85·5 per cent. had indices below 77·5, and of the 14·5 per cent. of skulls left only 3·7 per cent. had indices of 80 and upwards, while only ·4 per cent. had indices greater than 82·5. In the specially selected series 92 per cent.

had indices below 77·5; and only one skull, with an index of 80·9, rose into the conventional brachycephalic category.

The female group had a slightly greater tendency towards brachycephaly, with a mean index of 76·03. Ten skulls had indices over 80, but only one an index over 82·5. This and another skull were the only specimens which could be said to be true brachycephalic skulls. Comparisons between male and female skulls are instituted in the paper at some length, but here attention will be confined to the male group and to the data for the calvaria only.

The mean lengths in the two series differed by a millimetre only in favour of the West Scottish series. The mean basi-bregmatic heights were only fractionally different, but Turner's series exceeded the other by 5 mm. in mean breadth. The West Scottish skull has a mean capacity well up to the average of other European races, viz. 1459·4±4·11 in 405 males. The selected series had a mean capacity of 1511·3±8·6, the highest yielded by any other of the groups brought into comparison. The mean cephalic index of this group is 74·36 against 74·41 for the complete series. This shows that increase in capacity has no appreciable effect on the cephalic index. The series conclusively disproves the claim of greater capacity for brachycephalic skulls.

The maximum length in the male is greater than in any other series —European or otherwise—save the Whitechapel series described by Macdonnell, in which the mean was greater by a couple of millimetres. The mean of 405 male skulls was 187·52±·20, compared to 183·44 and 183·56 in the Tasmanian and Australian respectively.

The mean breadth is less, considerably, than it is in any other European series, viz. 139·56± 16, but greater than it is in dolichocephalic lower races. The Tasmanian breadth is 136·69±·44, and the Australian 130·60±·36.

The mean basi-bregmatic height in 405 male skulls was 132·72±·17, a relatively low figure. It is practically equal to the mean of the Whitechapel series, is slightly greater than it is in French and German skulls, but less than it is in modern Negroes, the Aino and Naquada races. The mean is practically equal in the West Scottish and Tasmanian skull, and only 3 millimetres greater than in the Australian.

There are only fractional differences in the basi-nasal lengths in the European series. In the lower races, as is well known, the basi-nasal length is absolutely greater than in the higher races, and this holds for the West Scottish as compared with the Tasmanian or Australian skull.

It follows from a consideration of the absolute measurements of the three main diameters that the West Scottish skull is longer, narrower, and lower than any of the Continental types available for comparison in

series; but, compared with the skull of the Tasmanian or Australian, it is longer, distinctly broader, and slightly higher, the basi-bregmatic height being taken as the measure of height.

The female skull is in the mean less capacious than the male, and the proportions maintaining between length and breadth are such that the female skull rises into the mesaticephalic category with a mean index of 76·03±·19.

The next section of the paper deals with the variability of the West Scottish skulls. A consideration of the data brings out the following as the most salient points: in all save 10 out of 49 characters—viz. cephalic index, height index, height-breadth index, palato-maxillary index, length of the occipital segment of the sagittal arc, basi-alveolar length, alveolar and nasal angles—the male skull showed greater variability than the female. In respect of nasal width, asterionic breadth, and basilar angle the variability was equal in both sexes. The series thus supports the older view regarding variability in the sexes, not the newer view of Karl Pearson and others that the female shows greater variability than the male.

Confining our attention to the larger series of male skulls, the coefficient of variability in the case of the capacity is relatively higher than in any series yet examined for this factor. The West Scottish skull is the least variable in length among other European series. It is *less* variable in respect of this character than the Australian, and equals in variability the Tasmanian skull. The coefficient for breadth is higher than the coefficient for length, but it is distinctly less than in the other European series; it is equal to the coefficient for the Tasmanian skull, but markedly greater than that for the Australian. Height shows a slightly lower degree of variability, and again the West Scottish and Tasmanian skulls closely correspond, while this time the Australian skull shows a higher degree of variability.

Although there are a number of exceptions, the general impression given by the tables is that the coefficients of variation are generally less than they are for the corresponding characters in other European series, and approximate to the values given for purer series such as the Tasmanian or Naquada. Where the Australian is included in the series it shows, except in the case of breadth, a higher degree of variability for the several characters than the West Scottish skull.

All this speaks for the uniform character of the series, and it demonstrates that the variability may be on the whole less, or as low, in a uniform series representing a race on a high level of civilisation, as in one on a low grade of culture. The higher degree of variability usually predicated for the higher races is probably a matter merely of admixture.

In the next section, on the correlation of the West Scottish skull, Dr Young shows that the male is more highly correlated than the female. In this his results are not in full accord with those of Pearson and Lee, but as the writer is not competent to judge the question on the mathematical side, the points on which the correlations touch the morphological side will be alone dealt with.

When the three main dimensions were correlated it was found that in both sexes length and breadth show the highest, and breadth and height the lowest correlation. When one dimension increases there is a tendency to increase in the other dimension correlated with it.

The series furnishes additional evidence against the "law of compensation." There is no evidence to show that, say, a breadth above the average is compensated by a height or length below the average. This may possibly, to some extent, apply when different skull forms are compared, but in a uniform series it does not hold at all. In the West Scottish series the maximum length and maximum breadth, as one would expect when basi-bregmatic height is the third factor, have a greater correlation to capacity than height, and breadth has a higher correlation to capacity than length. Minimum frontal width has an equal correlation to maximum length and to maximum width, showing that as the diameters increase all the dimensions enlarge.

The correlations of capacity to the cephalic and vertical indices are very small, and in some of the series compared with our own are actually negative. In the West Scottish series a slight positive correlation of $\cdot 091 \pm \cdot 033$ in the case of the cephalic index points to a very slight tendency towards brachycephaly, with increase of capacity. The series, however, affords no support, other than this, to Thomson's "elastic capsule" theory, nor to Lee's thesis that increase in capacity is associated with a greater emphasis of the form typical of the race. In our series the selected group of skulls with greater capacity has a mean cephalic index only fractionally less than the whole male group.

One of the most interesting points in this section of the paper is the demonstration of the part played by the occipital bone in expansion of the sagittal arc. The correlations are worked out for the sections of the arc to the total arc, and to the maximum length of the skull. It seems that, of the three, the occipital section has the highest correlation to the total arc. In other words, when the arc of the skull increases it is the occipital section which is responsible to the greatest degree for the increase, then follows the frontal, and then the parietal. The same holds for the female series, but in the female skull, while the correlations of the frontal and occipital sections are less than in the male, the correlation of the

parietal to total arc is equal in the sexes. In the same way the interparietal part of the occipital has a higher correlation to maximum length in the male, though apparently not in the female skull, than the frontal and parietal sections of the sagittal arc.

The correlation values are all comparatively low in the West Scottish series, a fact pointing to an infinite variety of minor differences or refinements of skull form in such a homogeneous series; because, as Dr Young says, it is apparently possible to have an alteration in a certain dimension with only a comparatively slight, though in most cases sensible, tendency to a corresponding increase in another dimension.

The remaining sections of the work comprise an elaborate morphological analysis of the characters of the cranial vault. For this purpose the methods of Klaatsch and Schwalbe were applied to the selected group of 100 male skulls. The only complete data available for comparison are those provided for us for the Tasmanian and Australian skull by Berry and his co-workers. Klaatsch's method has been applied to only one series of sufficient length, viz. to the Tasmanian skull, by Büchner, but Dr Young has worked out the data for the Australian skull on the profile outlines supplied by Berry and Robertson in their atlas. Professor Berry, in supplying other workers with this series of dioptrographic tracings, has done valuable service to craniology, and he has added to the obligation by granting in advance to them the free use of the figures. In Klaatsch's original description of his scheme of measurements, which is of course only an elaboration of older methods with less imposing names, he compared some individual Australian and European skulls, and reached conclusions which have not been confirmed in all respects by larger series of skulls. It must again be emphasised that Dr Young was working with the mean values of a homogeneous series of skulls dolichocephalic in type, and of large capacity. The comparison is instituted between this and the mean values of a series of skulls also dolichocephalic but of small capacity. The results might have been different had his series been brachycephalic in type, for it is probable that the factors involved in growth and expansion are different for this form of cranium.

Klaatsch took the glabella-lambda line as his horizontal base line, and found that when the basi-bregmatic line was drawn in on a sagittal contour, it cut this line at an angle of about 90° (fig. 1). In the Australian skull the angle varies from 84° to 94°, with a mean of 89·45°; in the Tasmanian the mean is 89·6°. In the Scottish series the angle varies from 87° to 100°, with a mean of 92·5°. The most frequent angle was 91°, and it occurred 21 times out of 100.

In the following abstract the comparison of the Scottish with the

Australian skull will be specially considered, but exactly the same results would come out in the case of the Tasmanian. The series from which the Australian means were derived was a mixed one containing a small proportion of female skulls. Dr Young separated the figures for the male skulls from those of the complete series in the case of Schwalbe's scheme, but not in the case of Klaatsch's method. The differences are merely fractional, and I shall here take the figures for the complete Australian series, for the sake of uniformity. It is the comparative, not the absolute, dimensions that are important. The glabella-lambda line is 7·5 mm.; the glabella-inion line 2·8 mm.; the maximum breadth 10 mm.; the basi-bregmatic height 3·7 mm.; the calvarial height 8·2 mm. greater in the Scottish skull. The frontal chord length is 4·8 mm., the glabella-bregma chord 5·3 mm. longer in the Scottish skull, but the parietal chords are practically equal in the two types. The lambda-basion line is 8·5 mm. longer in the Scottish skull, but the basion-glabella lines are approximately the same. The lambda-inion chord is as much as 12·7 mm. longer than in the Australian skull.

In the Scottish skull the height of the frontal arc is 21·6; of the parietal arc 23·3; of the occipital arc 9·7; and the corresponding figures for the Australian skull are 19·3, 22·9, and 5·7.

The frontal-arc index $\left(\frac{\text{height of arc} \times 100}{\text{length of arc}}\right)$ for the Scottish skull is 19·5, the parietal-arc index is 20·3, the occipital 14·8, while the corresponding figures for the Australian are 18·1, 20·2, and 10·9.

As far as these dimensions are concerned, the most striking differences between the Scottish and the Australian brain-case lie in the hinder part of the vault. The frontal bone is longer and more curved in the Scottish skull, the parietal bones are nearly identical in length and curvature, but the interparietal part of the occipital is much longer and more curved than in the Australian It will be remembered that this part of the occipital is more highly correlated to the total sagittal arc and to maximum length than either frontal or parietal.

Schwalbe's bregma and lambda angles each exceed by 2° the corresponding angles in the Australian, but the mean upper glabella angle of Klaatsch's figure is smaller in the Scottish skull. The total mean angles are nearly equal (74·4° to 74·9°), but there is a difference in the size of the components, the upper glabella angle being the larger in the Australian, the smaller in the Scottish skull. The total lambda angle is more acute in the Scottish skull, and its upper component is also more acute. The angle at the bregma is more obtuse by 2° than in the Australian, while the angles at the basion are equal or nearly so.

Lastly, the upper segment of the basi-bregmatic height is in the mean slightly less than the segment below the glabella-lambda line in the Scottish skull, while the opposite relation holds in the Australian. Now, if the central points be supposed to coincide, and the glabella-lambda line be taken as the base, and presumed to present the same inclination to the horizontal plane in both skulls, the low vault of the Australian skull would lead us to expect that the angle at the bregma would be more obtuse and the upper glabella and lambda more acute than in the Scottish skull, while

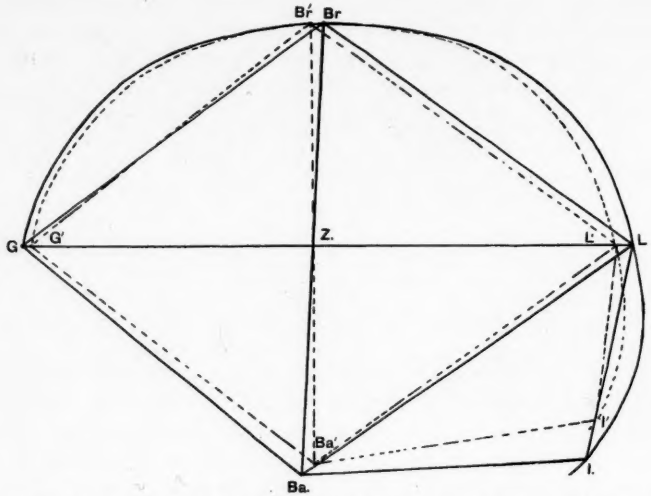

FIG. 1.—The sagittal contour of the mean Australian skull superimposed on that of the mean West Scottish skull, with Klaatsch's inscribed figure, the glabella-lambda line being taken as a common base and the central points made to coincide.

Continuous line = Scottish mean. Interrupted line = Australian mean.

the part of the height above the glabella-lambda line would be less than the lower segment. In the present case, however, the West Scottish skull takes in all these particulars the position that should be occupied by the Australian, and the Australian the place which should be occupied by the Scottish skull.

The reason for this is explained by the two diagrams. Fig. 1 shows the two mean contours and the contained polygons superimposed on the glabella-lambda line. The glabella-lambda arcs are very similar, and the height is the same in both; the centrum angle is greater in the Scottish skull, and the bregma is rather further back. The inion of the

Scottish contour is considerably depressed below the inion of the Australian contour, and the basion lies below and in front of the corresponding point in the Australian.

Fig. 2 shows the two contours superimposed on the glabella-inion line. It demonstrates how in the West Scottish skull the increase in the interparietal part of the occipital has raised the lambda, has uplifted and carried forward the bregma, so that the basi-bregmatic lines have become parallel and cut the glabella-lambda lines at nearly the same angles. The

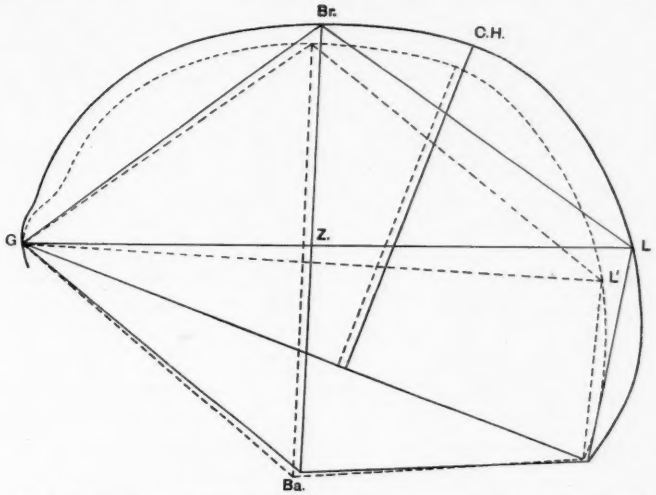

FIG. 2.—The same contours as in fig. 1, with their inscribed figures superimposed, the glabella-inion line being taken as a common base. The calvarial heights are also indicated.

Continuous line = Scottish mean. Interrupted line = Australian mean.

elevation of the lambda has given the glabella-lambda line a different inclination than in the Australian contour, and this in turn explains how, while Schwalbe's bregma angle is more obtuse in the Scottish skull, both upper glabella and upper lambda angles of Klaatsch's figure are more acute; and also how the angle at the bregma is more obtuse and the upper segment of the height shorter in the Scottish cranium.

The outstanding result that emerges from a comparison of the two figures is that the calvarial height measured from the glabella-lambda line is nearly the same in both types, and that the increase of the true calvarial height in the Scottish skull is due entirely to the increase in length of the lambda-inion factor. If we imagine the more capacious dolichocephalic

Scottish brain-case as the terminal phase in the expansion of a lowly, less capacious skull with the same mean dimensions as those of the Australian, we find that with increased capacity the parietal width has increased by about a centimetre and the length has increased by about 5 mm., due to the bulging of the part of the occipital bone related to the occipital lobes of the hemispheres. The elongated shape is retained, but as the increase in width is greater than in length the cephalic index is somewhat raised. The frontal and occipital regions have expanded with the parietal width, so that the norma verticalis presents a full oval outline. The basi-bregmatic height has enlarged by 3 mm. only, but the calvarial height, placed well back, has expanded by nearly a centimetre. With a general elevation of the vault, the greatest expansion has taken place not in the frontal but in the posterior part of the brain-box.

Translating these facts into terms of the brain, we may conclude that with a general expansion of the cerebral hemispheres there has been a specially great increase, and more particularly in depth, of the posterior parieto-occipital regions; and in explanation one's thoughts at once turn to the great co-ordinating field between the tactile, visual, and acoustic areas, the expansion of which has been responsible, as Elliot Smith has shown, for the pushing back and over on to the medial surface of the visual field in the human brain.

Those who are acquainted with the type of dolichocephalic skull represented in this West Scottish series are of course familiar with the fulness and depth of the hinder part of the brain-case and the prominence of the occipital probole, but this new demonstration of the factors involved in the growth and expansion of the dolichocephalic vault is important and suggestive.

Klaatsch's claim for the glabella-lambda line as a suitable horizontal base is not substantiated, and it has been demonstrated how comparatively similar the supra-glabella-lambda arcs are in the Scottish and Australian skulls. The uplifting of the vault has involved no expansion of the antero-posterior length of the parietal bone; a certain increase has occurred in the length and curvature of the frontal bone; a large increment has taken place in the length and curvature of the interparietal part of the occipital bone. It should be understood that these results apply only to the dolichocephalic form type, and that other factors may, indeed must, be involved in the growth and expansion of the brachycephalic form type of skull.

The next section of Dr Young's paper reveals some striking facts, perhaps the most important of the points raised by his work. All the skulls of the selected series of 100 specimens were divided by a fine saw cut

in the median plane. I believe no such long series of sagittal sections has been before examined and compared. The various angles were recorded, and Bolk's method for the determination of the position and inclination of the foramen magnum applied.

In this account I shall only refer to the results obtained respecting the spheno-ethmoidal and foramino-basilar angles. The results in respect of the first-named angle came rather as a surprise to me, but I can vouch for the correctness of the work, as I tested in nearly all the specimens the dimensions of the angle directly on the sections, and got the same figures as Dr Young did on his impressions.

In the first place, two outstanding types of base were met with, the flat and the steep. The spheno-maxillary angle varied from 136° to 170°, and the mean value was 152·35°, with a standard deviation of 6·58 and a coefficient of variation of 4·32. The range of variation is great, and the angle a relatively obtuse one. In some cases the angle was as great as the angles given for anthropoid skulls. Dr Young points out that a large angle might be reasonably assumed for a long basi-nasal length, and specimens were obtainable which illustrated this; but, on the other hand, other skulls, with approximately the same basi-nasal length, were found to show an angle diminished even to the extent of 34°. Two skulls were observed with the same glabello-occipital and basi-nasal lengths, but with spheno-ethmoidal angles differing by more than 20°. He worked out the correlations between the angle and basi-nasal length and maximum length, and discovered a very slight but positive correlation to basi-nasal length but not to maximum length, although, as had been shown earlier, there was a high correlation between the maximum and basi-nasal lengths. It may be noted that the nasion was used as the anterior extremity of the ethmoidal factor in the angle, and no doubt it is subject to some variation. The spheno-ethmoidal junction is also subject to variation, but in no case can the magnitude of the variation of the angle be explained by variations in the position of these two points. The wide differences in the angles are quite obvious, indeed striking, to the eye.

The foramino-basilar angle similarly varies within wide limits, having a range from 135° to 168°, with a mean of 147·68°. The difference between the two angles being 4·6°, the mean flexure of the cranial base falls short by that amount of 180°. The significance of this great range of variation of these angles is not obvious, and the subject wants further working out. In light of the results all comparative figures for the angles will require reconsideration. The slope of the foramen magnum is very variable, but, worked out according to Bolk's method, the mean

inclination forwards in the Scottish skull is less than in the Negroes examined by that author. It may be added that Dr Young has given some data regarding the thickness of the skull wall at various points.

A word in conclusion regarding the affinities of the West Scottish skull. As Dr Young points out, the skulls, as far as their main features are concerned, might be either Mediterranean or Teutonic. They most closely resemble, however, in all their characters the type of skull known as the long-barrow skull, and all the archæological and other evidence is in favour of the view that they represent the Mediterranean type of cranium which spread into our islands in the late Stone Age. The west of Scotland seems to have remained relatively true to the skull form of the early occupants of Dalriada, and this series is a local deposit, as it were, in nearly pure condition, of the primitive type of cranium.

THE ARTERIES OF THE PONS AND MEDULLA OBLONGATA: PART II.

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PART II.

THE PRECISE DISTRIBUTION OF THE ARTERIES SUPPLYING THE MEDULLA OBLONGATA AND PONS.

ALTHOUGH our knowledge of the gross anatomy of the bulbar branches of the vessels of the hind brain has hitherto been far from complete, it is vastly superior to the information we possess of the regions of the medulla oblongata and pons which these arteries supply.

Heubner (73), Duret (54), Kolisko (85), and particularly Beevor (19), have provided us with a considerable amount of information of the cortical and basal distribution of the cerebral arteries; and almost every anatomical text-book describes, in great detail, the precise blood supply of the fore brain. Alezais and d'Astros (5) have studied most carefully the vessels which supply the mid brain. As previously stated, the blood-vessels of the spinal cord have been fully considered by Marie (95), Obersteiner (102), Kadyi (82), Adamkiewicz (2), and Ross (115).

Yet the exact blood supply of the hind brain, by comparison, has been left in obscurity to this day; and no English manual of anatomy even attempts to unravel its mysteries, although its importance to the modern neurologist cannot be overestimated. This work, however, has not been wholly neglected, but within recent years it has become increasingly evident that the subject requires reinvestigation to elucidate the problems of clinical medicine. Enormous advances in our knowledge of the structure and functions as well as in the pathology of the central nervous system have been made since the arterial supply of the medulla oblongata and pons was last studied, and the importance and urgent desirability of further information are becoming more and more obtrusive. Our present knowledge is wholly due to the researches of Duret (55) and Adamkiewicz (2).

Duret's memoir was published more than forty years ago, when histological methods were very imperfect and the localisation of tracts was quite in its infancy. He made only twenty injections, and his attention was directed primarily to the radicular arteries. No attempt

was made to define the areas of the medulla and pons supplied by the individual vessels. Adamkiewicz, over twenty years ago, covered the same ground as Duret in his researches, but only advanced our knowledge by supplying a more detailed account of the course of the minute nutrient arteries within the bulb.

Both of these observers examined most carefully the small vessels supplying the cranial nerves, and traced their ramifications peripherally and centrally; but their work was essentially descriptive, for the knowledge of the structure and functions of the brain was not sufficiently extensive at that time to suggest the clinical significance such researches might have. This is another reason why it has failed to satisfy the demands of present-day neurology.

These two published accounts create the impression that the distribution of the arteries of the hind brain is extremely constant, and almost completely ignore the question of variation in supply.

The unsatisfactory state of our knowledge is manifest in almost every treatise or memoir on vascular lesions of the pons and medulla, and is the explanation of much of the vagueness in references to the subject when attempts have been made to explain the obscure etiology of so many bulbar diseases. Even if a greater knowledge did not prove of very great assistance in determining the etiology, it would at any rate prevent irrelevant allusions by which the physician and pathologist are able to throw the responsibility for their ignorance upon the unfortunate anatomist.

Technique.

About fifty injections in all have been made; but some of the earlier ones were not very satisfactory owing to defects in technique, which were remedied as the work progressed. At first it was intended to adopt completely Beevor's (20) method, in which he used a system of pressure bottles, and injected simultaneously several vessels. But this was not found to be feasible, owing to the small calibre and delicacy of many of the arteries in this region; instead, it became necessary to make the injections with a record syringe.

Beevor adversely criticises this method for the cerebral arteries, but it has been repeatedly proved, in the case of the arteries of the hind brain, that the resultant varying pressure did not cause any material inaccuracy in the field of injection. Even when two neighbouring vessels were injected, there was never the slightest confusion of the two colours along their line of contact. This fact lends support to the accepted opinion that the nutrient vessels to the pons and medulla oblongata are true "end-arteries."

Valenti and d'Alundo (146) studied the terminal branches of the cerebral arteries in mammals, especially the cat and the rabbit, and found that they anastomosed during intrauterine life, but after birth

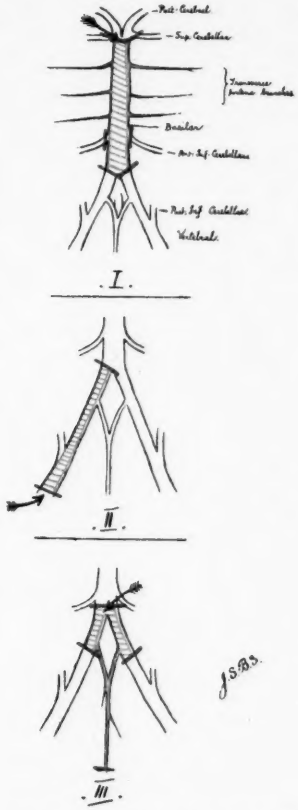

FIG. 6.—Method used for injection of I. basilar artery, II. vertebral artery, III. anterior spinal artery.

the communications were obliterated. Duret found that similar communications existed in the human fœtus during the third and fourth months of fœtal life.

As an essential preliminary to injection, the arteries were washed free from blood with saline solution. After the necessary ligatures had been applied, to prevent error from anastomoses or too widespread diffusion

of the stain, the needle was tied into the vessel and the brain placed in hot water in order to prevent the injection-fluid setting. In making the injection considerable pressure had to be exerted, and maintained for some time, if a complete and successful result was to be obtained. This was especially necessary in the case of the basilar artery, which proved to be much the most difficult to inject.

After withdrawal of the needle, the ligature fixing it was immediately tied to prevent escape of the stain, and the brain fixed in formalin for at least forty-eight hours.

After fixation, the bulbar or pontine branches were carefully studied and noted, as well as the anatomical disposition of the other vessels as described in Part I.

When the cerebellum had been removed, the stained portion of the floor of the fourth ventricle was accurately mapped out in diagrammatic form; and then serial sections of the medulla and pons were cut, figured, and mounted in order.

The sections were cut about one-sixteenth to one-eighth of an inch thick, and were fixed on sheets of glass.

Soluble colours in gelatine, as described by Beevor (20), were used for the injections.

Red and blue were chosen because they exhibit such a marked contrast, and the latter colour proved to be particularly satisfactory in the case of small areas, as its definition was so very clear.

Red. Carmine, ½ drachm.
Ammonia, ½ „
Glycerine, ½ ounce.

Blue. Nicholson's blue, 15 grains.
Alcohol (90 per cent.), ½ ounce.

In both cases dissolve, and then add to 2 ounces of gelatine dissolved in 1 pint of hot water.

Beevor (in 1907) was the first to employ soluble colours in his investigation of the cerebral vessels, but this method has never been adopted for the arteries of the pons and medulla; the greater accuracy obtained by using soluble colours, in preference to suspended insoluble powders, is quite obvious, and is referred to in Beevor's classical paper. Beevor claimed that all the colours, except the yellow (which has not been used in this work), were absolutely fixed by the formalin. My own specimens, although mounted in formalin, tend to fade slightly and lose their sharp definition at the periphery of the injected area; and I hear that the same difficulty is at present being experienced with Beevor's magnificent specimens in the Museum of the Royal College of Surgeons.

The Anterior Spinal Artery.

The bulbar distribution of this vessel is confined to the anterior and median parts of the medulla oblongata, and, owing to its remarkable constancy, it has been found preferable to consider it first, in order to simplify the descriptions of the less regular inconstant ones.

From the results of the seven experiments quoted by Moxon (100), there is good reason to conclude that the anterior spinal fills from above downward—a fact of considerable significance when clinically determining the result of its occlusion. The only variations in its distribution depended upon either an unusually low origin from the vertebrals (20 per cent. on the right and 13 per cent. on the left), or extreme caudal fusion of these two vessels, which was noted in 19 per cent. These two factors only influence the level of the upper limit of the area supplied, and in both cases cause the distribution to be less extensive when traced in a cephalic direction. In either instance the vertebral is found to compensate for the deficiency and to supply the region normally vascularised by the anterior spinal as the pons is approached.

In consequence of the diminutive size of the anterior spinal some difficulty was found in injecting it, which rendered it necessary to insert the needle at the junction of the two vertebrals, after applying ligatures below the origin of the artery under investigation. Thus the upper part of each vertebral was injected in addition to the anterior spinal. After ascertaining the area supplied by the vertebral in subsequent experiments, it was possible to eliminate that part of the medulla it supplied, and in that way obtain the exact distribution of the anterior spinal alone (see fig. 6).

Floor of the Fourth Ventricle.

Invariably the trigonum hypoglossi was accurately defined by the stain of the injection.

Spinal Cord.

In a number of injections it was possible to see the distribution to the first cervical segment of the spinal cord.

The grey matter of the anterior cornua and around the central canal was deeply stained; whereas the white matter of the ventral columns and the region of the anterior roots was stained a much paler colour. In addition, in about 50 per cent. the base of the posterior cornua was also injected. The median branches (set B) appeared to supply the grey matter, whilst the transverse rami (set C) provided smaller branches which ramified in the white matter and terminated in the grey matter; but their precise

anatomical arrangement and course within the cord have been admirably studied previously by others.

The more intense staining of the anterior cornua indicates its rich blood supply, which has been demonstrated by Ross (115) and subsequent observers.

The above description is in perfect agreement with the opinion of Kadyi (82), Adamkiewicz (3), Obersteiner (102), and Marie (95), but, in addition to the support it lends to their work, it also gives a clearer and probably more accurate conception of the region supplied by the anterior

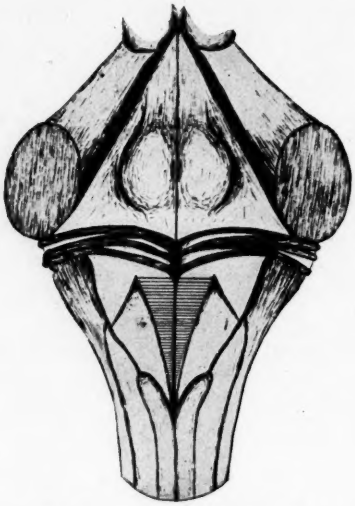

Fig. 7.—Floor of fourth ventricle.

system of spinal arteries; because the observations are made before it becomes obscured by the anastomoses between the anterior and posterior systems, which occur below this level. In the investigation of the distribution of the anterior spinal to the cord, this vessel has never been injected as far as the point where it communicates with the posterior spinal, and consequently the stained area must strictly represent the district supplied by the former vessel alone.

This subject is somewhat controversial, and often rendered obscure by many writers in their endeavour to divide the cord into three districts—first the part supplied by the anterior system, secondly the part supplied by the posterior, and lastly the area supplied by both. The latter, accord-

ing to Kadyi, approximately amounts to one-third of the transverse area of the cord.

Level of Pyramidal Decussation.

The median set of bulbar branches can be seen with a lens to turn obliquely in a dorsal direction amongst the decussating fibres, which they supply as far back as the crossed pyramidal tract, where they terminate. The detached head of each anterior cornu and the grey matter surrounding the central canal, as well as the ventro-lateral ground bundles, the nucleus

FIG. 8.—Cervical spinal cord.

FIG. 9.—Decussation of pyramids.

and tractus solitarius, Gower's tract, and (of course) the remains of the pyramid were also supplied. The latter two were chiefly dependent upon the smaller perforating branches of the transverse rami.

Level of Sensory Decussation.

The area of distribution at this level was very similar to the previous one; the only additional structures supplied were the internal arcuate fibres as they cross the middle line to form the medial lemniscus, and the nucleus of the hypoglossal nerve.

Calamus Region.

Here the district supplied by the anterior spinal was limited laterally by the fila of the hypoglossal nerve as they passed to their superficial origin, and dorsally by the nuclei of the posterior columns, which were never included. At this level the dorsal nucleus of the vagus, in addition to the hypoglossal nucleus, pyramid, medial lemniscus, tecto-spinal tract, and medial longitudinal bundle, was within the injected area, but the tractus solitarius was usually situated laterally to it.

Mid-Olivary Region.

In this section the ventral part of the inferior olive with the olivo-cerebellar fibres, as they passed out of the hilum to reach the opposite

FIG. 10.—Normal distribution of anterior spinal artery.

inferior cerebellar peduncle, and the medial accessory olive were supplied, as well as the structures supplied in the calamus region. That is to say, at this level the pyramid, hypoglossal nucleus, ventral part of the inferior olive, and the whole of the formatio reticularis alba on each side are supplied by the anterior spinal.

There was every indication that the median branches formed a network and richly supplied the hypoglossal nucleus, as described by Duret. The majority passed dorsally, through the lemniscus, to this nucleus, but a certain number turned into the hilum of the inferior olive, the ventral

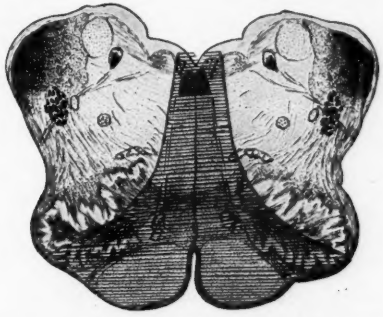

FIG. 11.—Normal distribution. Mid-olivary region.

part of which they were found to supply. The transverse set provided shorter branches, which penetrated the pyramids and the ventral external arcuate fibres, even to a point just dorsal to the antero-lateral sulcus.

The upper group of branches (set A), as described in Part I., formed a plexus on the upper part of the pyramids, and supplied a similar area to the parent vessel, above its origin from the vertebrals.

Upper Olivary Region.

Hitherto it has been found unnecessary to refer to the variations signified at the outset of the description of the distribution of this artery. Normally the anterior spinal continued to supply the same region as described in the previous section as far, in a cephalic direction, as the level of the entrance of the auditory nerve, at which point it was replaced by the vertebral. In cases of low origin of the anterior spinal, or where the site of junction of the two vertebrals was considerably below the inferior border of the pons, the former artery was found to supply the bulb only as far as a point somewhere between the lower border of the pons, and the upper third of the olivary eminence. The exact level of this point obviously depended upon the extent of the variation in the two factors which have been stated to affect its distribution.

Under no circumstances was the anterior spinal found to supply any region above the level of the lower border of the pons, or, in other words, no injection is to be seen in a transverse section displaying the striæ

medullares; but their position is so liable to variation that it is preferable to adopt the first method of description.

Normally, in the cephalic direction, the distribution of the anterior spinal became slightly reduced, and was gradually replaced by bulbar branches of the vertebral (set A) and the basilar.

It is instructive to note that the hypoglossal nucleus, the origin of nerves, primarily spinal, which later became cranial, is supplied by the anterior spinal artery.

The Vertebral Artery.

In the early part of the work this vessel was injected from above, but, owing to the imperfect injection of the most cephalic set of bulbar branches by this method, it was found advantageous to insert the needle of the syringe below, immediately above the place where the artery had pierced the dura.

The distribution of this artery was subject to very considerable variation, which has been found to depend upon three factors:—

1. *Variation in the distribution of the posterior inferior cerebellar artery.*—Attention has already been drawn to the fact that the vertebral replaces the bulbar branches of this vessel when it is absent or fails to provide any nutrient twigs for the supply of the medulla, and compensates almost invariably for their insufficiency. The effect of this will be shown to be most obvious in the olivary region.
2. *The origin of the anterior spinal artery.*—When this vessel arises at the level of the lower extremity of the olive, or below that point (20 per cent. on the right and 13 per cent. on the left), the vertebral has to compensate for its deficient supply to the most cephalic part of the medulla.
3. *The level of the junction of the two vertebral arteries.*—When the junction occurs some distance below the caudal border of the pons (19 per cent.), the distribution of the vertebral and anterior spinal is curtailed, and that of the basilar increased; whereas, in cases where the junction was distinctly above this point (8 per cent.), the area supplied by the vertebral was increased, with a corresponding decrease in that supplied by the basilar.

The latter two factors will influence the cephalic limit of distribution.

The percentage variation in the distribution of the vertebral, together with the factors which cause it, is of enormous clinical interest, and helps to elucidate many of the outstanding difficulties that arise in connection

with the localisation of the occlusion of vessels in this region. Attention must be directed again to the division of the bulbar branches of the vertebral into three sets (upper, middle, and lower), as a clear conception of their arrangement makes the involved description somewhat less complex.

Floor of the Fourth Ventricle.

The injection always demarcated the trigonum vagi and, usually, the trigonum hypoglossi in the neighbourhood of the striæ acusticæ. There

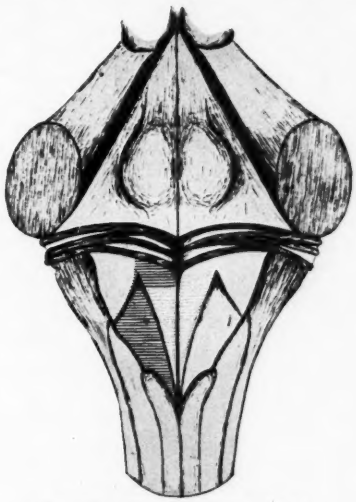

FIG. 12.—Floor of fourth ventricle.

was rarely some extension to the trigonum acustici and the inferior part of the colliculus facialis. The staining of the latter region was only seen in cases where the two vessels united cephalic to the lower borders of the pons.

Level of Pyramidal Decussation.

At this level the most caudal set of branches have been seen to enter the lateral region of the medulla. They are found to supply a triangular interval having its apex towards the central canal, which was bounded ventrally by the detached head of the anterior cornu and decussating fibres, and dorsally by the funiculus cuneatus.

This area included the spino-cerebellar tract, remains of the posterior cornu, substantia gelatinosa of Rolando, nucleus and tractus spinalis

nervi trigemini, and a few of the fibres which formed the lateral cerebro-spinal tract.

When the posterior spinal arose from the vertebral (on the right in 18 per cent. and on the left in 20 per cent.), and was also injected, the funiculi gracilis and cuneatus with their nuclei were also stained; and consequently

FIG. 13.—Decussation of pyramids.

the whole area of the medulla, at this level, was supplied by the vertebral arteries and their two spinal branches. It is quite inconceivable that such a widespread occlusion could occur clinically.

Level of Sensory Decussation.

The distribution here was very similar to that seen in the previous section, only the tract of Gowers was also supplied, as, at this level, it is found to be situated in a more lateral position, owing to the occupation of the ventral region by the motor fibres.

Calamus Region.

Here the area supplied was the same as the above, with the addition of the nucleus and tractus solitarius, in those cases in which they did not lie within the anterior spinal district (see p. 261). Hitherto no variation of any moment has been described, unless we include the posterior spinal, which is, strictly speaking, a separate artery with a definite distribution of its own, and the supply has been provided practically by the caudal set of bulbar branches.

Mid-Olivary Region.

At this level the study is restricted to the distribution of the middle set of vessels, composed of branches passing chiefly to the postero-lateral sulcus. They are the branches which vary according to the distribution of

the posterior inferior cerebellar artery, and consequently considerable variation in the vertebral supply is to be expected.

When the posterior inferior cerebellar freely provided branches for the retro-olivary region, the area supplied by the vertebral was represented by a narrow "wedge" between the anterior spinal district medially and that of the posterior inferior cerebellar dorso-laterally. This wedge included the medial and ventral parts of the formatio reticularis grisea, the dorsal half of the inferior olive, and frequently the dorsal vago-glossopharyngeal nucleus. The injected portion of the formatio reticularis grisea included the fasciculus tegmento-olivaris, the olivo-cerebellar fibres, and the dorsal accessory olive.

The wedge increased in size proportionately to the decrease in the

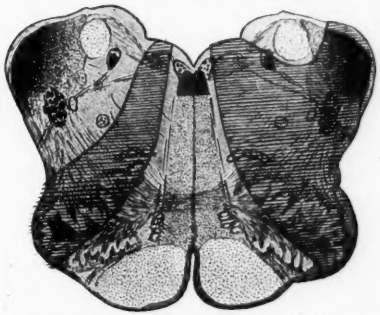

FIG. 14.—Absence of posterior inferior cerebellar on right. Mid-olivary region.

area supplied by the posterior inferior cerebellar, so that, in the absence of the latter vessel, the whole of the dorso-lateral region of the bulb was dependent upon the distribution of the vertebral. The significance of the percentage variation in distribution of the posterior inferior cerebellar now becomes manifest. According to the figures stated, some increase in the area supplied by the vertebral, at this level, was to be found in 36 per cent. on the right, and 32 per cent. on the left; but in the vast majority of these the posterior inferior cerebellar failed to provide any bulbar branches, so that in 31 per cent. on the right and 29 per cent. on the left the vertebral was found to supply the whole of the formatio reticularis grisea in this region. Therefore, in the latter number, the vertebral also supplied the spino-thalamic, rubro-spinal, and the anterior and posterior spino-cerebellar tracts, as well as the nucleus ambiguus, descending root of the vestibular nerve, nucleus and tractus spinalis nervi trigemini, and a large part of the inferior cerebellar peduncle. This variation, dependent upon the distribution of the posterior inferior cerebellar, will be main-

tained as far as the pons; but, for brevity, future reference to it will be omitted.

Upper Olivary Region.

We now gradually come to the consideration of the upper set of bulbar branches.

FIG. 15.—Normal distribution of vertebral artery.

From this level the wedge-shaped area was seen to increase medially owing to the diminishing anterior spinal district, and laterally at the expense of the posterior inferior cerebellar district, when traced in a cephalic direction. The whole of the inferior olive was supplied, and

the more lateral part of the pyramid, together with an increasing amount of the formatio reticularis grisea. At this level normally a considerable amount of the inferior cerebellar peduncle was supplied by the vertebral, and consequently the diminishing posterior inferior cerebellar district was situated between two parts of the area supplied by the former artery.

Lower Border of the Pons.

Normally, at the most cephalic limit of the medulla, the vertebral completely replaced the anterior spinal and posterior inferior cerebellar arteries. So that, in addition to the whole of the formatio reticularis alba, including the medial lemniscus, dorsal longitudinal bundle, tecto-spinal

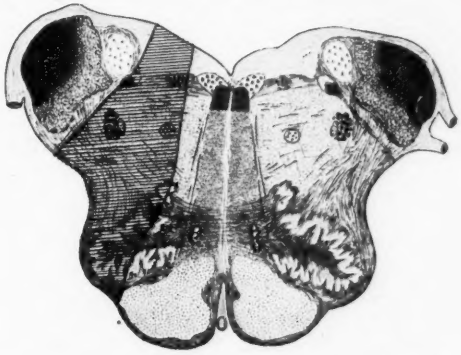

FIG. 16.—Variation dependent upon low origin of basilar (19 per cent.).

tract, and the most cephalic part of the hypoglossal nucleus were also almost entirely supplied by the vertebral. Consequently, just at this level, practically the whole of the medulla was supplied exclusively by the upper set of bulbar branches from the two vertebral arteries.

Provided the arteries maintain what is described as their normal arrangement, the only structures ever to be found outside the vertebral district were the inferior cerebellar peduncle, which may be supplied by the posterior spinal or posterior inferior cerebellar, the most medial portion of the pyramid supplied by the anterior spinal, and perhaps more frequently a small part of the retro-olivary region supplied by the posterior inferior cerebellar artery.

The above account is only for the normal arrangement and distribution, and even that is not quite constant; the two factors which cause variation in the vertebral supply in the upper part of the medulla have still to be considered. From the foregoing it can be seen easily that abnormally

low origin of the anterior spinal will cause the vertebral to take over at a lower level, and consequently more completely, the supply of the pyramid hypoglossal nucleus and the tracts contained in the formatio reticularis alba.

The low junction of the two vertebrals, unless the origin of the anterior spinal is abnormally low (an association which is of extreme rarity), will result in the basilar replacing the anterior spinal. Consequently, in 19 per cent. the vertebral failed to supply the pyramid, hypoglossal nucleus, and formatio reticularis alba, and its occlusion would not cause hemiplegia, as is generally thought to be the inevitable result of such a lesion.

When the vertebrals fused abnormally high (8 per cent.) they replaced the

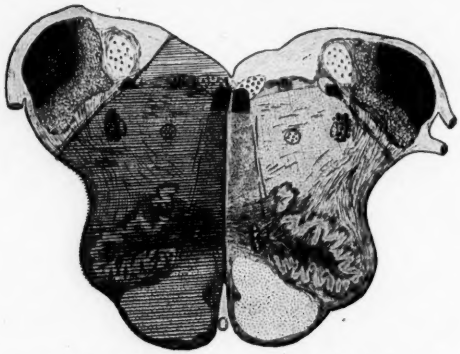

FIG. 17.—Variation dependent upon low origin of anterior spinal.

basilar caudally, and supplied the pyramidal bundles and medial lemniscus in the pons, together with the abducent nucleus and fibres of the facial nerve. The more caudal part of the abducent nucleus has been supplied occasionally by the vertebral in cases where this vessel terminated normally at the lower border of the pons. The specimens produced strong evidence to support the opinion that the terminal ramifications of the median bulbar and pontine branches spread out and run for some distance, in a cephalic direction, in the grey matter of the floor of the fourth ventricle. This is indicated by the persistence, repeatedly, of some injection in this situation in sections cut cephalic to the lower border of the pons, *i.e.* the upper limit of the normal distribution (see fig. 15).

The only alternative to this supposition is that the median vessels do not run directly dorsally, but incline slightly in a cephalic direction as they pass towards the floor of the fourth ventricle.

The deep staining of the nuclei in the floor of the fourth ventricle

supported the opinion expressed by previous writers that there is a vascular network in this situation, which is formed by the terminal ramifications of the median nutrient branches from the various arteries.

The Posterior Inferior Cerebellar Artery.

Considerable attention has been directed to this artery, first, because of its increasing clinical importance, and secondly, because our unsatisfactory and incomplete anatomical knowledge of its distribution demands revision and additional research. It has long been known that it supplied branches to the retro-olivary region of the medulla, but even Duret and subsequent anatomical observers have failed to determine the precise extent of, or variation in, its distribution, as it is only during recent years that it has sprung into such remarkable eminence.

Eight years ago Burrows, at Thomas' (140) instigation, made some injections to illustrate its distribution, but neglected to study the variation in its supply: although reference to the literature on the subject of the clinical manifestation of its occlusion demonstrates clearly that its distribution cannot be constant.

For a similar reason, Wallenberg's (148) study of this artery fails to provide the necessary knowledge which modern neurology demands. Anatomical research alone can explain the discrepancies in the symptomatology of the numerous reported cases of occlusion of the posterior inferior cerebellar artery.

Reference to Part I. will show how frequently the vessel was absent, and how commonly (31 per cent. on the right and 29 per cent. on the left), when present, there was an absence of bulbar branches to the retro-olivary region. Furthermore, in 5 per cent. on the right and 3 per cent. on the left it will be seen that these branches were inefficient, and only entered the most caudal part of the postero-lateral sulcus, and consequently merely supplied a small area of the bulb. This variation has been seen to depend very largely upon the course of the artery, as it curves round the medulla to reach the inferior surface of the cerebellum. The other important factor which influenced its distribution was the origin of the posterior spinal artery, which arose from the posterior inferior cerebellar in 73 per cent. on either side.

Excluding the district supplied by the posterior spinal, the usual distribution of the vessel under consideration is confined to the limits of the inferior olive. The majority of its bulbar branches entered the postero-lateral sulcus, but some certainly penetrated dorsal to this point and passed into the inferior cerebellar peduncle. These branches did not

appear to bear any marked relation to the vagus and glossopharyngeal nerves, as indicated by Duret, although some might be termed "radicular."

Mid-Olivary Region.

This is the most typical section in which to see the district it supplies, as the latter is at its maximum, and decreases when traced from this point in either a caudal or a cephalic direction.

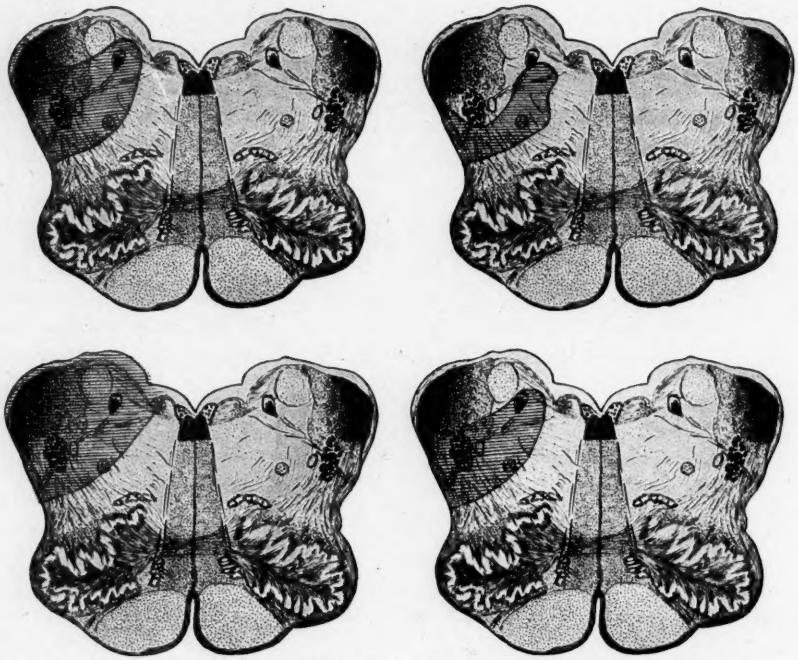

FIG. 18.—Four variations in the distribution of posterior inferior cerebellar. Mid-olivary region.

The injected area was limited ventrally by the inferior olive, except laterally, where the tegmento-olivary tract invariably intervened, and medially by the fibres of the hypoglossal nerve. Dorsally its limits were not so well defined. Usually the ventral part, at least, of the inferior cerebellar peduncle was injected, and frequently part of the dorsal vago-glossopharyngeal nucleus and a small portion of the descending root of the vestibular nerve. Thus it was seen that the posterior inferior cerebellar

artery, at this level, supplied most of the formatio reticularis grisea—all except that part included in the vertebral district. Consequently its obstruction will affect the spino-thalamic, anterior spino-cerebellar, and rubro-spinal tracts, the olivo-cerebellar fibres, as well as the dorsal nucleus, or fibres, of the glossopharyngeal and vagus nerves, nucleus ambiguus, and the more ventral part of the inferior cerebellar peduncle. When the artery maintained its more normal course and distribution, the nucleus and tractus spinalis of the trigeminal nerve were also invariably supplied. This is in contradiction to the opinion expressed in an early paper (30), but more extensive investigation has proved that the spinal nucleus and tract are only excluded from the posterior inferior cerebellar district when the bulbar branches of this vessel are reduced in number, as a result of its more irregular course.

The variation at the mid-olivary level, and the compensatory increase of the area supplied by the vertebral, have been fully considered with the distribution of the latter vessel.

Above and below the level considered, the posterior inferior cerebellar district became gradually reduced; in the former direction it was replaced by the vertebral and basilar, and in the latter by the vertebral alone. It is important to note that it is the more central part of the formatio reticularis grisea which is persistently injected in both directions, and consequently the spino-thalamic and rubro-spinal tracts and the nucleus ambiguus were supplied most extensively by the posterior inferior cerebellar artery.

The Posterior Spinal Artery.

The small size of this vessel prevented its separate injection. But, owing to its very constant distribution, it was easily possible to appreciate its own district when it was injected along with either the posterior inferior cerebellar or vertebral arteries. It arose from the former in 73 per cent. and the latter in 27 per cent., but appeared to be frequently absent, when it was usually replaced by supernumerary short bulbar branches from the vertebral.

Normally it has been seen to bifurcate into an ascending ramus, which was somewhat inconstant, and a descending ramus, which commenced the tortuous posterior spinal chain.

The descending ramus supplied the funiculi gracilis and cuneatus with their nuclei, and in all cases where the branch was present this distribution was found to be absolutely constant. The ascending ramus was more variable. It usually supplied the caudal and dorsal part of the inferior cerebellar peduncle, but, in addition, occasionally provided branches for

the descending root of the vestibular nerve and the trigonum acustici. In the absence of the ascending ramus, small branches from the descending limb of the posterior inferior cerebellar arteries replaced its supply for the inferior cerebellar peduncle and part of the descending root of the vestibular nerve.

From the foregoing accounts it will be seen that the blood supply of the inferior cerebellar peduncle is both complex and subject to very considerable variation. Caudally (at its origin) it was normally supplied ventrally by the posterior inferior cerebellar, and dorsally by the posterior spinal. Usually in the cephalic direction both arteries were replaced gradually by the vertebral and, to a less extent, by the basilar.

FIG. 19.—Normal distribution of posterior spinal.

Quite frequently the anterior inferior cerebellar, or even the internal auditory, provided for the inferior cerebellar peduncle a few branches, which merely augmented those supplied by the other vessels, and which were not of the same clinical importance as the latter.

The Basilar Artery.

More failures have occurred in the injection of this artery than in any of the others. This was apparently due to the greater difficulty experienced in removing the blood from the numerous small pontine branches, and the considerable and prolonged pressure required to inject satisfactorily the perforating branches of the transverse pontine rami.

The only factor which materially affected its distribution was the

variation in the level of its formation by the two vertebral arteries. This has been very fully discussed previously.

Floor of the Fourth Ventricle.

The striæ acusticæ and that part of the ventricular floor situated cephalic to them were usually stained.

The colliculus facialis on each side, and the most medial part of the

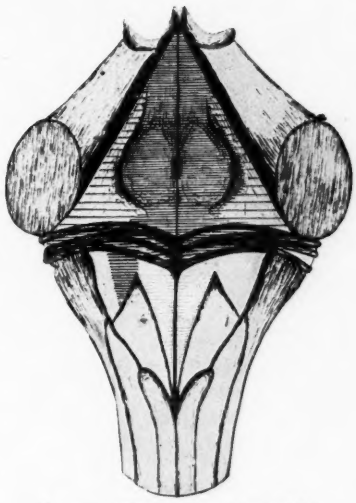

FIG. 20.—Floor of fourth ventricle.

floor, were supplied by the median pontine branches, and the more lateral parts by the perforating branches of the transverse rami.

Frequently the more medial part of the trigonum acustici was injected in addition. When the vertebral arteries fused some distance below the caudal border of the pons, the most cephalic part of the trigonum hypoglossi was also stained.

Upper Limit of the Medulla.

Normally the medial part of the pyramids and the ventral portion of the formatio reticularis alba were injected; but if the level of the formation of the basilar was caudal to the more usual point, this artery

was found to have replaced completely the vertebrals. In a few cases where the posterior inferior cerebellar supplied inefficient bulbar branches to the upper part of the postero-lateral sulcus, the basilar was found to replace it at this level, and consequently supply the whole of the formatio reticularis grisea, and the inferior cerebellar peduncle.

Obviously the various pontine branches of the basilar must, practically alone, supply under normal conditions the whole of the pons; consequently it will only be necessary to describe separately the distribution of the

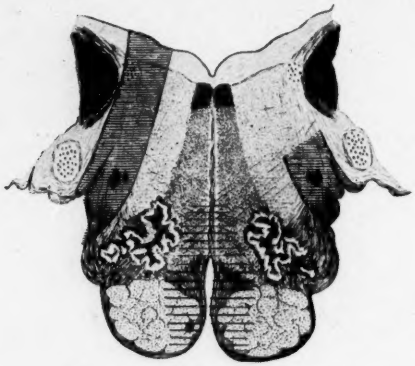

FIG. 21.—Upper limit of medulla.

median and transverse sets, instead of continuing the method adopted for the other arteries.

The *median set* supply the structures immediately lateral to the middle line in the tegmental part, and the greater proportion of the pyramidal bundles and transverse pontine fibres in the basilar part as well as the more medial part of the corpus trapezoidum.

The injected portion of the tegmental part will include the nuclei of the abducent trochlear and oculo-motor nerves, and the fibres of the facial nerve which are in such intimate relation with the former, the medial longitudinal bundle, the medial lemniscus, and the tecto-spinal and thalamo-olivary tracts.

The perforating branches from the *transverse set* supply the more lateral parts of the pons.

Within their field of injection are to be found: the brachium pontis, lateral part of the corpus trapezoidum, superior olive, and the nuclei of the fifth, seventh, and eighth cranial nerves.

In 19 per cent. the origin of the basilar was abnormally low, and consequently it replaced the vertebral above, and supplied the pyramids, formatio reticularis alba, and the most cephalic part of the hypoglossal nucleus, as well as a variable part of the lateral portion of the upper medulla.

In 8 per cent., owing to the cephalic origin of the basilar, it failed to supply the caudal part of the pons, including the facial and abducent nuclei.

Anterior Inferior and Superior Cerebellar Arteries.

No definite distribution to the pons can be given in the case of either of these two vessels.

The former often assists the posterior inferior cerebellar by providing branches for the upper and dorso-lateral part of the bulb, which supply a variable part of the inferior cerebellar peduncle and the descending

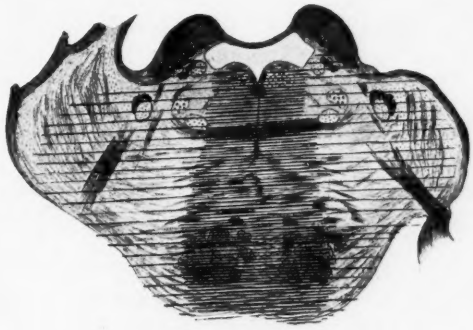

FIG. 22.—Pons.

root of the vestibular nerve. It frequently gives a variable number of branches to the lateral and caudal part of the brachium pontis, as it passes on to the inferior surface of the cerebellum.

The superior cerebellar artery has been shown, by Alezais and d'Astros, to supply branches to the region of the inferior colliculus, but it also frequently gives a few branches to the lateral and cephalic part of the brachium pontis, although no precise area of distribution can be defined.

SUMMARY.

1. The *anterior spinal* supplied—

(*a*) *In the cord:*

(1) Anterior and base of posterior cornua.
(2) Grey matter around central canal.
(3) White matter of ventral columns and region of anterior roots.

(*b*) *In the medulla:*

(1) Pyramids and pyramidal decussation.
(2) Medial lemniscus and tecto-spinal tract.
(3) Dorsal longitudinal bundle.
(4) Hypoglossal nucleus (except cephalically).
(5) Nucleus and tractus solitarius (at decussation).
(6) Gowers' tract (at decussation).
(7) Dorsal nucleus of vagus (at calamus region).
(8) Olivo-cerebellar fibres as they cross the middle line.
(9) The internal and ventral external arcuate fibres with nucleus.

2. The *vertebral* supplied—

(1) Few pyramidal fibres at formation of lateral cerebro-spinal tract.
(2) Pyramids at the lower border of pons, and a variable part of the lateral part below.
(3) The whole of the ventral part, and the cephalic portion of the dorsal part, of the inferior olive.
(4) The dorsal accessory olive.
(5) Tegmento-olivary tract and olivo-cerebellar fibres in formatio reticularis.
(6) Generally the dorsal vago-glossopharyngeal nucleus above the calamus region.
(7) Most cephalic part of hypoglossal nucleus.
(8) Nucleus and tractus solitarius (at calamus).
(9) Nucleus and tractus spinalis nervi trigemini (at decussation).

When it replaced the posterior inferior cerebellar it also supplied:—the spino-thalamic, rubro-spinal, and anterior and posterior spino-cerebellar tracts, nucleus ambiguus, descending root of the vestibular nerve, and nucleus and tractus spinalis of the trigeminal nerve, as well

as part of the inferior cerebellar peduncle. In 8 per cent., owing to the high level of fusion to form the basilar, the vertebral supplied the abducent and facial nuclei as well as the other more medial structures in the lower part of the pons.

3. The *posterior inferior cerebellar* supplied—

(1) Spino-thalamic tract.
(2) Rubro-spinal tract.
(3) Olivo-cerebellar fibres as they passed to inferior cerebellar peduncle.
(4) Dorsal vago-glossopharyngeal nucleus or the emerging fibres of the vagus and glossopharyngeal nerves.
(5) Nucleus ambiguus.
(6) Nucleus and tractus spinalis of trigeminal nerve.
(7) Ventral part of inferior cerebellar peduncle.

4. The *posterior spinal* supplied—

(1) Funiculi and nuclei gracilis and cuneatus.
(2) Caudal and more dorsal part of the inferior cerebellar peduncle.
(3) Occasionally part of the descending root of the vestibular nerve.

5. The *basilar* supplied—

(*a*) *Medial set of pontine branches:*

(1) Abducent nucleus and trochlear nucleus.
(2) Oculo-motor nucleus (caudal part).
(3) Medial longitudinal bundle.
(4) Medial lemniscus.
(5) Tecto-spinal tract.
(6) Thalamo-olivary tract.
(7) Transverse pontine fibres.
(8) Medial part of corpus trapezoidum.

(*b*) *Transverse set of pontine branches:*

(1) Brachium pontis.
(2) Lateral part of corpus trapezoidum.
(3) Superior olive.
(4) Facial nucleus.
(5) Remaining nuclei of eighth nerve.
(6) Remaining nuclei of fifth nerve (including motor nucleus).

When the origin of the basilar was abnormally low (19 per cent.) it supplied the pyramids, medial lemniscus, tecto-spinal tract, dorsal longitudinal bundle, and most medial part of the hypoglossal nucleus, together with a variable part of the lateral portion of the upper medulla.

6. The *anterior inferior cerebellar* supplied a variable part of the most caudal portion of the brachium pontis and upper and dorso-lateral limits of the medulla.

7. The *superior cerebellar* supplied a variable part of the most cephalic portion of the brachium pontis.

In Memoriam.

PRINCIPAL SIR WILLIAM TURNER, K.C.B., F.R.S., ETC.
1832–1916.

THE eve of the Jubilee year of this Journal is sorely clouded by the lamented death of our Senior Editor. As the few survivors (if there be any besides myself) will recollect, the project of founding the Journal originated with him. Some of his earlier papers were published in the *Natural History Review*, and the demise of that periodical in 1865 left the way open for a special Journal for the publication of papers on Anatomy and Physiology.

During the committee meetings preliminary to the British Association at Nottingham in 1866, at which Humphry presided over the Physiological Section, Turner enlisted Humphry's support for his scheme, and they took into their counsel two of the editorial staff of the defunct review, Newton and Perceval Wright, and also, at Professor Humphry's suggestion, John Willis Clark. At that meeting all the arrangements were finally completed.

Turner was keenly interested in promoting the success of the Journal. Visiting Edinburgh in that year, I found him occupied in preparing the first number. We spent some time together in compiling a list of names of those who might be asked to contribute papers. He was then thirty-four years old, but looked older. Already he had made his mark in anatomical literature, and was regarded as the coming leader among British anatomists. That position he certainly occupied during the larger part of the last half century.

Although his name will be hereafter always associated with Scotland, and especially with the Edinburgh School, Turner was English by birth and education: a native of Lancaster, where he was born in 1832, and a student at St Bartholomew's from 1850 to 1854. That, on his transplantation to Scotland, he easily and rapidly assimilated to his new surroundings is not really surprising, for the difference between the people of Northern England and those of the Lothians is rather one of environment than of race.

During his student days at Bart's he had attracted the notice of

Sir James Paget, who was sponsor for his first paper, on "The Cerebro-spinal Fluid," published in the *Proceedings of the Royal Society* for 1854. In that year the Edinburgh Professor of Anatomy, John Goodsir, passed through London, returning from a long sojourn on the Continent, and took the opportunity of consulting with Paget as to the selection of an assistant. On his recommendation, Goodsir chose Turner (who had in 1853 obtained the M.R.C.S.) for the post. He had also been awarded honours in Chemistry at the London University, where later he graduated M.B. in 1857.

The young demonstrator early showed his aptitude for research, and, in the interval between his appointment and the foundation of this Journal, had written nineteen papers on many branches of the Science—Anomalies of Muscles, Histology of Nerve, the Pancreas, Variations in Vertebræ, Fossil Human Crania, etc.

Owing to the ill-health of Professor Goodsir most of the teaching of Anatomy fell to the share of the demonstrator, and his reputation soon spread far beyond the bounds of the University as an able, keen, thorough, and systematic teacher. He had, by nature, that royal gift of being able to recognise his students when he met them out of class: no mean power when the numbers with which he had to do are considered.

Goodsir died in 1867, and Turner was triumphantly elected as his successor. There were two other candidates, but the result of the election was a foregone conclusion. This chair he held for thirty-six years, during which he raised the Anatomical School of Edinburgh to the rank of the foremost, as well as the largest, in Britain.

Another side of his character soon showed itself. He had established his reputation as a researcher and as a teacher, but it became obvious to all associated with him that he was also an accomplished man of affairs. Being returned by the Universities of Edinburgh and Aberdeen as their representative on the General Medical Council in 1873, it was not long before his fellow-councillors recognised that he had a clear perception of, and a sound judgment concerning, the several problems with which the Council had to deal. As a testimony to his qualities as a wise statesman and a systematic and judicious man of business, he was elected by the Council, in 1898, as their President, and continued to hold that office until 1905.

In 1903 the Principalship of Edinburgh University became vacant by the death of Sir William Muir, and the Board of Curators

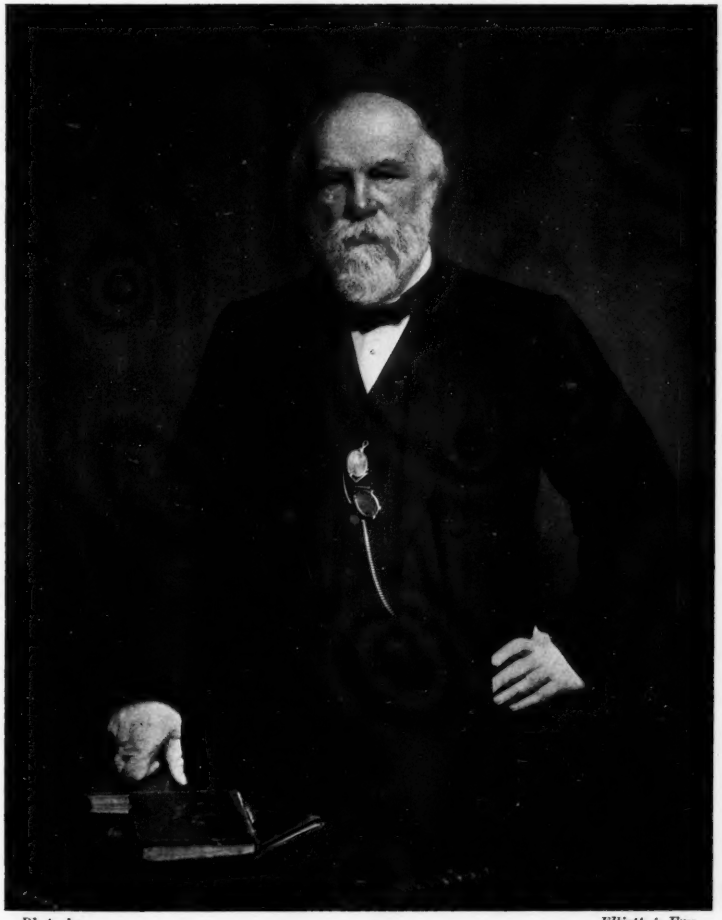

Photo by *Elliott & Fry.*

PRINCIPAL SIR WILLIAM TURNER,
K.C.B., M.B., F.R.C.S. L. and E., LL.D., D.C.L., D.Sc., F.R.S.,
Knight of the Royal Prussian Order *Pour le Mérite.*

showed their wisdom by electing Sir William Turner to fill the post. No better appointment was ever made. The thirteen years during which he presided over the University were, until the outbreak of the war, years of prosperity and advance. The great new buildings for the Medical School and the M'Ewan Hall are the best material testimony to the success of his work in the promotion of its interests.

While he was thus sustaining his great name as an administrator and statesman, he still continued to contribute many and valuable additions to the literature of anatomical research. It is needless to specify these individually. They are known to all readers of this Journal. I may especially mention those on anthropology, placentation, cranio-cerebral topography, the anatomy of cetacea and of sharks. His last great work on Scottish anthropology was published in 1915. In recognition of his scientific contributions to knowledge he was elected a Fellow of the Royal Society in 1877. He received the honour of knighthood in 1886, and was created K.C.B. in 1901, the year after he had been President of the British Association. He also received the Prussian Order *pour le Mérite*.

This is not the place to recount the very long catalogue of honorary degrees and honorary memberships of foreign and colonial societies which were his. Few names are more widely known, as there is scarcely any part of the world in which his students are not to be found. He easily held the record of being the greatest of our educators of the anatomical teachers of the English-speaking world; at least nineteen of his students became Professors of Anatomy or of kindred subjects in Britain, America, Australia, South Africa, and other countries. This success was partly due to the reputation of the Edinburgh Medical School, which for many years has numbered among its professors some of the most distinguished authorities in almost every subject of the medical curriculum, partly to the fact that Scottish medical graduates are numerically preponderant in our colonies and dependencies; but largely to the systematic, clear, and methodical character of his teaching, which was so widely appreciated that electors to teaching posts naturally gave preference to those that had been his pupils. An interesting testimony in this respect was the great Festschrift edited by Professor Cunningham, the *Textbook of Anatomy*, in which the eleven sections were written by eleven of Sir William's former demonstrators.

For the last twenty years he has looked old, although hale and fairly active. For some years he had found it beneficial to spend part of the winter in the south of Europe, where the conditions of climate were less rigorous than they are in Edinburgh. In a letter written to me late last year he expressed his regret that he could not go to Italy this winter. He was, however, able to discharge his official duties until a few days before the end. At a meeting of Senators on February 3 he felt unwell, and returned home before the conclusion of the meeting. The illness gradually became more serious and troublesome gastric symptoms appeared. He passed away quietly in his sleep on February 15.

Even to the end he retained his interest in the Journal, and every sheet of each issue passed through his hands before going to press. To all who knew him his death is a sore personal grief.

A. M.